Macroinvertebrate assemblages in Andean Patagonian rivers and streams: environmental relationships

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Abstract

Macroinvertebrate communities from 29 streams and rivers of the mountain and the Andean Patagonian Plateau were analyzed. Samples were collected from six river basins, which were part of four different biozones of the Patagonian Ecoregion. Samples from mountain streams were dominated by Plecoptera, Ephemeroptera, Trichoptera and Diptera, while plateau rivers where mainly Diptera, Oligochaeta and Mollusca. Total invertebrate abundance ranged from 7 to 12 249 ind.m^{-2}. Elmidae, *Paratrichocladius, Chironomus, Smicridea annulicornis*, *Parasericostoma ovale* and *Meridialaris laminata* were the most abundant insect taxa, while *Nais communis* and *Hyalella curvispina* were the most abundant non-insect taxa. Species-environmental relationships were examined using Canonical Correspondence Analysis. Current speed, conductivity, substrate size and abundance of aquatic plants, were identified as the major variables structuring faunal assemblages. Regression analyses revealed that species richness was negatively correlated with latitude, and positively correlated with water temperature and altitude. Macroivertebrate abundance increased with conductivity, altitude and water temperature. These results suggest that habitat heterogeneity was the strongest predictor of macroinvertebrate assemblages, but species richness could be predicted at a landscape scale using topographical and climatic features.

Introduction

The structure of macroinvertebrate communities has been the subject of much research in river systems. Potential benefits of research on macroinvertebrates include the quick assessment of biological resources for conservation purposes and the detection of pollution through differences between predicted and actual faunal assemblages (Ormerod and Edwards, 1987). Pristine environments in remote areas are suitable for the detection of environmental changes (Cantonati & Ortler, 1998) and some studies have been carried out to assess the effects of global climate change on high-latitude freshwater systems in northern regions (Oswood et al., 1992; Hauer et al., 1997). Understanding of stream biodiversity patterns has been heavily by local studies of small temperate forested streams, and few studies have been carried out across

broad spatial scales (Vinson & Hawkins, 1998). Difficulty in sampling across heterogeneous habitats and in the identification of specimens after collection makes studies at broad spatial scales difficult and expensive.

Classification and ordination techniques based on species and environmental data have shown the existence of patterns that could be used in streams to typify assemblages and to predict faunal composition at different sites on the basis of known values of environmental variables (Malmqvist & Mäki, 1994; Burian, 1997).

Several intensive and extensive surveys have been carried out in lotic environments of Patagonia (Wais, 1985, 1987, 1990; Wais & Bonetto, 1988; Di Persia, 1991; Miserendino, 1995). Distribution patterns of macroinvertebrates along altitudinal gradients have been analyzed (Albariño, 1997; Miserendino, 1998; Miserendino & Pizzolón, 2000 a, b). Some func-

tional and ecological aspects have also been studied (Modenutti et al., 1998; Albariño & Smirez, 1998). However, few studies have been carried out in Patagonian Plateau rivers (Wais, 1990), and structure and macroinvertebrate composition of streams in high latitudes of this region are unknown.

The Andean Patagonian region presents two distinct areas: the mountain chain and the plateau. Several fluvial systems originate in the Andes Range and flow to the west to drain into the Pacific Ocean. Other river basins drain through the plateau into the Atlantic Ocean. From different topographical and phytogeographical areas, 29 rivers were sorted in a 1000-km transect between the cities of El Bolsón and Calafate. Our objectives were to: (1) describe macroinvertebrate assemblages and their composition; (2) determine the environmental variables that best define environmental-gradient along which macroinvertebrate community changes and (3) identify abiotic factors that best predict species richness and abundance of macroinvertebrates.

Study area

The mountain chains and several eastern foothills characterize the Patagonian Andes. They are spread across 2000 km from Neuquén to Tierra del Fuego. Maximum elevations in the area can exceed 3600 m a.s.l. The climate is classified as temperate cool, and rainfall decreases dramatically eastward from the mountains to the Atlantic Ocean. Some sites in the mountain chain receive 3000-mm yr^{-1} precipitation, while low temperatures and high drought characterize the steppe, in which precipitation can be 100–150 mm yr^{-1}. Geomorphologic features and local climatic characteristics determine four biozones: (1) Andean-Humid, (2) Sub-Andean Sub-humic, (3) Extra-Andean oriental and (4) Extra-Andean occidental (Del Valle et al., 1995; Paruelo et al., 1999).

This strong climatic gradient has originated two main phytogeographical provinces: the Sub-Antarctic Forest and the Patagonian Steppe. Perennial (*Austrocedrus chilensis* (D.Don.) Pic. Serm. & Bizzari, *Nothofagus dombeyi* (Mirb.) Blume and *Maytenus boaria* Molina.) and deciduous species (*N. pumilio* (P et E.) Krasser, *N. antarctica* (Forst. f) Oerst.) constitute the sub-Antarctic forests. The deciduous tree locally named lenga (*N. pumilio* (Poepp. et Endl.) Krasser) covers drainages of low-order streams. Some ecotone watercourses are mainly flanked by *Salix fra-*

gilis L. and *S. nigra* Marsh. The lack of precipitation on the Patagonian Plateau causes vegetation coverage of xerophytic forms. *Mulimun spinosum* Pers., *Stipa* spp., *Senecio* spp., *Colletia spinosissima* Gmel., *Adesmia* sp., *Fabiana imbricata* Ruiz et Pay. and *Poa* sp. represent the herbaceous-shrub-like steppe (Tell et al., 1997).

The 29 sampled streams were on the east side of the Andes between 41° 53′ S, 71° 29′ W and 50° 25′ S, 72° 27′ W (Fig. 1). They ranged in altitude from 175 to 750 m a.s.l. (Table 1). Mountain rivers have a pluvionival regime, with two seasonal peaks in flows. One peak is due to heavy winter precipitation and the other to melting ice and snow on the Andes. Steppe rivers are fed by the pluvial precipitation from the west. The study region has a high degree of continentality and several small watercourses are covered by ice in winter.

Puelo-Manso, Futaleufú-Yelcho and Corcovado-Palena basins drain into the Pacific Ocean. Futalaufquen Lake is located in Los Alerces National Park, this is one of the largest lakes in the Futaleufti-Yelcho basin. Chubut, Senguerr, Deseado and Santa Cruz basins drain into the Atlantic Ocean, and the plateau is the main geomorphic structure in their run through the sub-Andean steppe. Two big glacial lakes are included in the Santa Cruz basin: Viedma and Argentino. They have been fed by the ice melting in the Pleistocene. A 2000-km² coverage of great glaciers and continental ice is present in the southwest of the Santa Cruz province and this area is part of Los Glaciares National Park. The study sites were placed in areas without human impact. The main land use in the region includes cattle raising and forestry.

Materials and methods

Field methods

Watercourses were sampled once in April 1996. Macrozoobenthos was collected with a Surper net (30 × 30 cm, mesh size 250 μ). Care was taken to include all possible microhabitats over representative sections of the stream. In the big rivers, only the littoral section was sampled to a depth of 45 cm. At each site, 10 sampling units were taken and pooled for analysis. Samples were fixed with 47% formalin solution. At the laboratory, samples were elutriated and then passed through a series of sieves (mesh width 250–1000 μm). Detritus occurring in the samples were

Table 1. Environmental features of the 29 Patagonian rivers. (April 1996). Biozones: Andean Humid Megabiozone (1); Sub-Andean Sub-Humid megabiozone (2); Extra-Andean Megabiozone: occidental (3) and Oriental (4). Phytogeographical regions: *Nothofagus* forest 1, Patagonian steppe: 2 (Subandme sector) and 3 (Central sector). (*) littoral (-) without data

Site number	Stream:	Latitude (S)	Longitude (W)	Biozone	Phytogeog Region	Aq. plants abundance (%)	Altitude (m a.s.l.)	Stream order	Wet width (m)	Depth (cm)	Velocity (m s^{-1})	Air temperature (°C)	Water temperature (°C)	Conductiv. μS cm^{-1}	Substrate Index	Wood (DM g m^{-2})	Leaves (DM g m^{-2})	FPOM (DM g m^{-2})
1	Quemquemtreu	41° 53 ′	71° 29′	2	1	0	456	4	30	35	1.50	20	16	40	8.5	3.77	0.49	2.74
2	Chubut	42° 10′	71° 10′	3	2	50	700	4	60	40	0.28	18	17	68.1	6.5	0.48	0.05	0
3	La Cascada	42° 53′	71° 36′	1	1	0	550	2	7	27	1.11	19	14	34.4	8.5	17.71	3.80	0.56
4	Desaguadero	42° 53′	71° 37′	1	1	0	500	2	23	37	1.21	19	16	48.8	6.5	3.11	2.60	3.12
5	Centinela	42° 50′	71° 38′	1	1	0	600	3	7	26	1.53	20	10	41.2	8.5	12.62	2.52	0.82
6	Fontana	42° 56′	71° 36′	1	1	0	650	2	7	24	1.05	18	10	30.6	7	–	–	–
7	Rañinto	42° 54′	71° 36′	1	1	0	650	1	15	31	1.11	19	9	38.2	8	20.08	1.34	0.24
8	Blanco	43° 12′	71° 35′	1	1	0	425	2	15	20	0.57	18	12	36	8.5	–	–	–
9	Baguilt	43° 12′	71° 33′	1	1	0	400	4	18	35	0.81	18	12	34.6	8.5	0.91	3.96	0.21
10	Los Rifleros	43° 11′	71° 31′	2	1	10	425	1	9.3	7.8	0.56	18	12	92	6	–	–	–
11	Nanty Fall	43° 10′	71° 31′	2	1	10	400	3	8	28	0.41	18	14	95	5.5	0.09	0.14	0.11
12	Frío	43° 21′	71° 30′	1	1	50	570	3	13	18.5	0.40	20	14	88	6	11.30	0.35	2.93
13	Tecka	43° 28′	70° 50′	3	2	80	660	4	3	24.8	0.66	10	8	173	5	0.32	<0.05	3.77
14	Cherke	44° 01′	70° 45′	3	2	5	730	4	10	35	0	12	8	130	5.5	<0.05	<0.05	0.74
15	Verde	45° 05′	70° 45′	3	2	20	690	2	7	28.7	0	13	9	169	6	<0.05	<0.05	1.54
16	Senguerr	45° 02′	70° 51′	3	2	0	690	4	80	33	1.30	13	10	25.4	6.5	1.25	<0.05	0.60
17	Mayo	45° 40′	70° 17′	3	3	80	470	5	20	16.5	0.51	15	10	236	5.5	–	–	–
18	Fénix Grande	46° 35′	70° 55′	3	3	0	200	3	18	18.4	0.44	14	7	77	5	–	–	–
19	Pinturas	46° 56′	70° 42′	3	3	20	600	2	1.5	9.3	0.22	15	10	309	5.5	<0.05	<0.05	<0.05
20	Ecker	47° 7′	70° 52′	4	3	40	600	3	21	21.6	0.33	13	7	102	5	–	–	<0.05
21	Chico	48° 26′	70° 37′	4	3	0	450	4	60	93	0.75	6	5	74	6.5	<0.05	<0.05	0.65
22	Diablo	49° 17′	72° 55′	1	1	20	750	2	10	32	0.29	10	7	20	7.5	0.17	0.06	1.26
23	del Puesto	49° 17′	72° 54′	1	1	5	750	2	6	25	1.66	9	4	28.6	8.5	15.71	1.93	0.77
24	de las Vueltas	49° 18′	72° 54′	1	1	0	750	5	30	35	1.87	10	7	34.8	8.5	2.29	0.32	<0.05
25	Cangrejo	49° 36′	72° 17′	2	3	30	250	2	14	19.25	0.43	11	10	37	8	0.40	<0.05	0.20
26	Chalía	49° 35′	71° 30′	4	3	30	250	2	14	14	0.30	9	8	87	4	<0.05	<0.05	0.07
27	Las Leonas	50° 10′	72°	4	3	0	250	5	100	40*	0.69	10	8	44.6	5	0.73	0.07	2.70
28	Santa Cruz	50° 15′	71° 54′	4	3	0	175	6	200	40*	2.50	13	8	39	5	–	–	<0.05
29	Mitre	50° 25′	72° 27′	1	1	0	250	2	30	34.6	1.36	21	9	57.6	8	2.32	7.61	0.23

divided into fine (250–1000 μm) and coarse (>1000 μm) particulate fractions (FPOM and CPOM, respectively). After that, coarse organic material was divided into: wood, leaves and others (grass, roots, buds) (Voelz & Ward, 1990). All fractions were dried (60 °C for 24 h) and weighed.

Remnant material was placed in shallow white trays and all macroinvertebrates were sorted out, they were stored in 70% ethyl alcohol with the addition of glycerin. All invertebrates were identified to the lowest possible taxonomic level using regional keys (Domínguez et al., 1994; Lopretto & Tell, 1995). Macroinvertebrate abundance was obtained by counting all individuals in a taxon and expressing the results as number m^{-2}.

Stream order was obtained after Strahler (1957). Elevation, latitude, longitude and basin location were taken from maps (1:50 000, 1: 100 000 and 1:

250 000) and available references were also consulted (Coronato & Del Valle, 1988; Paruelo et al., 1999). Substrate composition was estimated as percentage of each fraction: boulder, cobble, gravel, pebble and sand. The relative proportion of substrate was assessed using a grid (1 m^2) (Gordon et al., 1994), in the big rivers only the dominant substrate of littoral zone was recorded. Substrate was also classified giving a weighed index increasing with particle size (Rodriguez & Wright 1988). At each site, air and water temperatures were measured with a mercury thermometer ($-10/+60°$ C). The atmospheric temperature in Patagonia depends on the latitude and elevation, and in summer the meridian gradient varies 0.8 °C for each degree of latitude (Del Valle et al., 1995). Previous surveys in Patagonian streams showed that March and April results in relatively constant environmental conditions (water temperature and flow) (Miserendino, 1998).

Average depth was calculated from five measurements from one transversal profile across the channel with a calibrate stick. Since the sampling was carried out in a low water period, surface current speed was obtained by timing a bobber (average of 3 times) as it moved over a distance of 10 m (Gordon et al., 1994). Macrophytes, filamentous algae and aquatic mosses were ranked as percentage of coverage. Main species of riparian vegetation were recorded. Water samples were collected below the water surface and kept at 4°C in a Styrofoam box prior to analysis. After that, samples were transferred to the laboratory and conductivity was measured within a period of four days using a conductimeter HORIBA U-7. Conductivity in Patagonian streams shows very little variation within this time due to mesosilicic rocks which are dominant in the area (Pizzolón, pers.comm.).

Data analysis

Environmental variables and macroinvertebrate abundance data were log (x+1) transformed prior to statistical analysis to normalize and stabilize the variance. To explore the response of macroinvertebrates, a PCA and a CA on abundance data were performed, and these preliminary analyses showed that macroinvertebrate variation was better described by unimodal models than by linear models. A canonical correspondence analysis (CCA) was carried out (Ter Braak, 1986) using the package CANOCO (Ter Braak & Smilauer, 1999). This method expresses the main relations between species and environmental variables

by combining ordination and regression (Ter Braak, 1986). To detect significant environmental covariables, a Pearson correlation matrix with Bonferroni-adjusted probabilities was calculated. The variables longitude, biozone and air temperature were omitted before the CCA analysis was done. To extract a reduced variable set, covariable environmental factors were excluded if the variable inflation factor was greater than 10 (Ter Braak & Smilauer, 1998). After that, the variable wet width was omitted and a set of 13 environmental variables was used to perform the final CCA analysis (Table 1).

In the CCA biplots, the 1st and 2nd axes represent the most important environmental gradients along which macroinvertebrate species are distributed. The direction of each environmental vector represents the maximum rate of change for that particular environmental variable and its length indicates its relative importance to the ordination. The significance of all primary CCA axes was determined by the Monte Carlo permutation testing (199 permutations) of the eigenvalues (Ter Braak, 1999).

Simple-linear regression analyses were plotted to explore relationships between species richness, abundance and environmental variables. Total abundance was log (x+1) transformed. Predictive models were inferred using stepwise-multiple regressions.

Results

Rivers and streams environmental features

The substrate type was highly diverse, ranging from mud to boulders and bedrock. Stream orders ranged from 2 to 6 and wet width ranged from 7 to 200 m. Since sampling was carried out in the low-water period, current speed was 0 m s^{-1} in some plateau rivers. Mountain streams with high channel slopes exhibited more than 2.50 m s^{-1} water velocities. Water conductivity ranged from 20 to 309 μ S cm^{-1}. In general, plateau rivers showed higher conductivity than mountain streams (Table 1). Watercourses located in the *Nothofagus* forest showed greater riparian coverage than ecotone or plateau's rivers, which were predominantly in grasslands.

Macroinvertebrate assemblage structure

Altogether, 95 taxa of macroinvertebrates were identified. Aquatic insects were mainly Ephemeroptera, Diptera and Coleoptera. However, *Nais communis*

was the most abundant species. Rithral environments were mainly Plecoptera, Ephemeroptera, Trichoptera and Diptera. The Plecoptera were mostly *Klapoteryx kuscheli, Senzilloides panguipulli, Chilenoperla puerilis, Potamoperla myrmidon* and *Limnoperla jaffuelli.* Plecoptera were common in rocky bottom streams rather than in sandy and muddy bottoms. They were also absent in Cherke and Verde rivers, which did not show water movement. Five species of *Baetis* were identified, and they were distributed in several kinds of rivers (Table 2). However, the leptophiebids, *Meridialaris chiloeensis* and *M. diguilina* were very frequent. Ephemeroptera were absent only in Verde River. *Smicridea annulicornis, Cailloma* sp. and *Parasericostoma ovale* were the most frequents Trichoptera. Trichoptera were absent in Blanco, Fenix Grande, Chico and Chalia rivers.

Elmidae was the most frequent and abundant Coleoptera. *Paratrichocladius* sp. 2 was the most ubiquitous dipteran (21 rivers), followed by the Tipulidae *Hexatoma (eriocera)* and the Athericidae *Dasyoma* sp, *Chironomus* sp., *Pentaneurinii* sp. and *Ablabesmyia* sp. were recorded mainly in backwaters, that probably presented low dissolved oxygen. The amphipod *Hyalella curvispina* was present in 11 rivers, and was very abundant in Cherque River followed by Pinturas and Ecker Rivers. Water conductivity of these rivers was 102–309 μS cM^{-1} with patches of *Myriophillum* sp. and *Cladophora glomerata.*

Seventeen species were only restricted to the plateau river. *Chironomus* sp., *Rheotanytarsus* sp. and *Pentaneurini* sp. were the Chironomidae more frequently collected at these sites. The Dytiscidae *Lancetes* sp. and the Gyriidae *Andogyrus ellipticus* were also recorded; however, they showed low density. The Hyriidae *Diplodon chilensis* was the only mollusk exclusively recorded in the plateau rivers. The Aeglidae *Aegla neuquensis,* was recorded in both Tecka and Mayo rivers, in which water conductivity was higher than 170 μS cm^{-1}.

Species numbers observed per stream ranged from 4 to 28 (Fig. 2). The minimum number of species was found in the Fenix Grande river where a gravel-sand bottom occurred. The maximum number of species was found in one small (Tecka Stream) and one medium-sized (Frío River) stream, both with aquatic plants.

Densities of macroinvertebrates averaged 1353 ind m^{-2} over the whole study. Most of the rivers showed density values minor than 1000 ind m^{-2}. The Fenix Grande river showed the lowest value of dens-
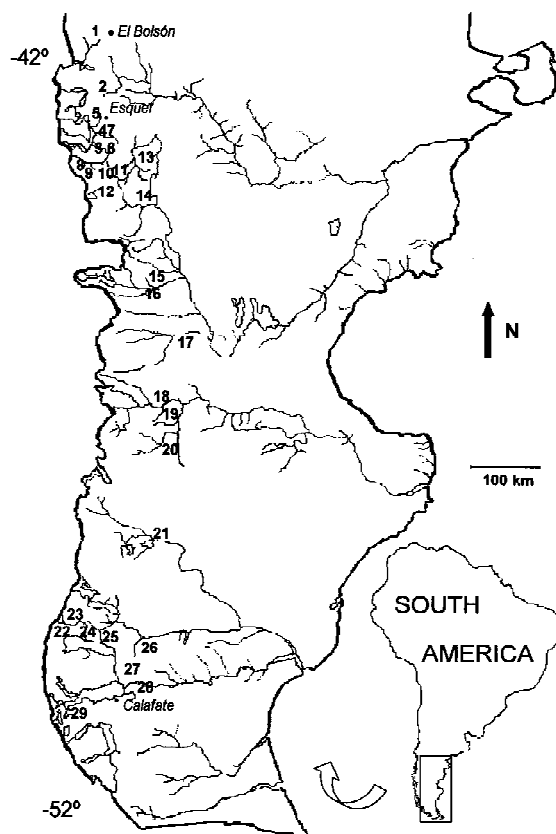

Figure 1. Study area showing the locations of the 29 survey streams and major waterways within the Patagonia Ecoregion, Argentina. Names of the rivers are in Table 1.

ity (7 ind m^{-2}) and the highest (12 249 ind m^{-2}) one was recorded in the Mayo river, in which Nais communis was the most abundant invertebrate (Fig. 2). Other rivers with high densities of macroinvertebrates were the Pinturas, Cherke and Frío, these rivers were dominated by Elmidae, *Hyalella curvispina* and *Parasericostoma ovale,* respectively.

Environmental relationships

The results of the CCA ordination for 95 macroinvertebrate species, 29 rivers and 14 environmental variables showed that only 35.1% of the variance in species abundance was accounted by the first four ordination axes (Table 3). This was expected because of the high level of environmental noise intrinsic to this type of data. CCA resulted in a significant model as was shown by the Monte Carlo Test. The first ordination axis reflected a gradient mostly related to current velocity, substrate size, aquatic plant abundances and conductivity (Figure 3A). Water conductivity and the

Table 2. List of macrozoobenthos species found in 29 Patagonian rivers. The habitat units used:(A) rocky bottom streams in *Nothofagus* forest (<10 m), (B) Rivers (>10 m) in *Nothofagys* forest, (C) Rivers in grassland (>10 m (D) plateau rivers and (E) littoral of big rivers. In brackts: species codes used in CCA analysis

Species	Hab. Un.	Species	Hab. Un.
Plecoptera		Chironomidae	
Austroperlidae		*Paratrichocladius* sp1 (Pasp1)	ABCD
Klapopteryx kuscheli Illies (Kk)	AB	*Paratrichocladius* sp2 (Pasp2)	ABCDE
Klapooteryx armillata Navás (Ka)	AB	Orthocladinae sp1 (Osp1)	CDE
Perlidae		Orthocladinae sp2 (Osp2)	DC
Pictetaperla gayi Pictet (Pg)	AB	Orthocladinae sp3 (Osp3)	AC
Kempnyela genualis Navás (Kg)	ABC	Orthocladinae sp4 (Osp4)	A
Grypopterigidae		Orthocladinae sp5 (Osp5)	BE
Notoperla sp (Nsp1)	AB	*Chironomus* sp (Chi)	D
Notoperla archiplatae Enderlein (Na)	A	*Rheotanytarsus* sp (Rheo)	D
Notoperlopsis femina Illies (Nf)	AD	Pentaneurini sp (Pensp1)	D
Antarctoperla michaelseni Klapálek (Ami)	ACE	*Pentaneura* sp (Pensp2)	AD
Antarctoperla sp (Anc)	BCD	*Ablabesmya* sp (Abl)	ACD
Limnoperla jaffueli Navás (Lj)	ABD	Simuliidae	
Aubertoperla kuscheli Illies (Ak)	A	*Simulium* sp (Sim)	ABC
Potamoperla myrmidon Mabille (Pm)	ABCD	*Gigantodax* sp (Gig)	ABE
Senzilloides panguipulli Navás (Sp)	AB	*Cnesia* sp (Cne)	
Pelurgoperla personata Illies (Pp)	A	Tipulidae	
Chilenoperla puerilis Illies (Cp)	ABD	*Hexatoma* (eriocera) sp (Hex)	ABCD
Notonemouridae		*Limnophila* sp1 (Lph1)	AB
Udamocercia arumifera Aubert (Ua)	AC	*Limnophila* sp2 (Lph2)	C
Araucanioperla bulocki Navás	A	*Molophilus* sp (Mol)	A
Ephemeroptera		Athericidae	
Ameletopsidae		*Dasyoma* sp (D)	ABCD
Chiloporter eatoni Lestage (Ce)	ABC	Empididae	
Baetidae		Empididae sp (Emp)	ACD
Baetis sp1 (Bsp1)	ABCD	Muscidae	
Baetis sp2 (Bsp2)	ABD	*Lispoides* sp (Lis)	DE
Baetis sp3 (Bsp3)	ABCE	Syrphidae	
Baetis sp4 (Bsp4)	ADE	Syrphidae sp (Syr)	D
Baetis sp5 (Bsp5)	CDE	Ceratopogonidae	
Caenidae		Ceratopogonidae sp (Cer)	AD
Caenis sp (Cae)	D	Tabanidae	
Leptophebiidae		Tabanidae sp (Tab)	D
Meridialaris laminata Ulmer (Ml)	ABCDE	Blephariceridae	
Meridialaris chiloeensis Demoulin (Mc)	ABCDE	*Edwardsina (Edwardsina)* sp (E)	A
Meridialaris diguilina Ulmer (Md)	B	Psychodidae	
Rhigotopus andinensis Pescador & Peters (Ra)	AD	Psychodidae sp (Psy)	AD
Penaphlebia chilensis Eaton (Pc)	A	**Coleoptera**	
Penaphlebia vinosa Demoulin	A	Elmidae	
Nousia bella Pescador & Peters (Nb)	ABCD	Elmidae sp (Elm)	ABCDE
Nousia minor Demoulin (Nm)	C	*Austrelmis* sp (Aul)	AC
Trichoptera		Dytiscidae	
Leptoceridae		*Lancetes* sp (Lan)	D
Brachisetodes major Schmid (Bm)	ABCD	Gyrinidae	
Nectopsyche sp (Nec)	A	*Andogyrus ellipticus* Brullé (Ae)	D

Table 2. Continued

Species	Hab. Un.	Species	Hab. Un.
Sericostomatidae		**Anisoptera** sp (A)	D
Parasericostoma ovale Schmid (Po)	BCD	**Odonata** sp (O)	D
Myotrichia murina Schmid (Mm)	A	**Arachnida** (Or)	D
Hydrobiosidae		**Crustacea**	
Cailloma sp (Cai)	BCDE	*Hyalella curvispina* Shoemaker (Hc)	ABCDE
Neoatopsyche chilensis Schmid (Nchi)	ACD	*Aegla neuquensis* Schmitt (Ae)	D
Australochorema rectispinum Schmid (Are)	AE	**Oligochaeta**	
Rheochorema sp (Rh)	ABE	Lumbriculidae sp (Lum)	ABCD
Rheochorema lobuliferum Flint (R1)	ABC	Tubificidae	
Hydropsychidae		*Limnodrilus variegatus* Müller (Lv)	BC
Smicridea annulicornis, Blanchard (Sa)	BCDE	*Limnodrilus udekemianus* Claparede (Lu)	D
Glossossomatidae		Naididae	
Glossossomatidae sp (Glo)	AE	*Nais communis* Piguet (Nc)	D
Limnephilidae		**Hirudinea**	
Limnephilidae sp (Lim)	D	Glossiphonidae sp (Gl)	BCD
Monocosmoecus sp (Mon)	AD	**Platyelmintha**	
Hydroptilidae		*Girardia* sp (Gi)	D
Hydroptila sp (Hid)	AD	**Mollusca**	
Oxyethira sp (Ox)	ABCDE	*Chilina patagonica* Sowerby (Chp)	ACD
Ochotrichia sp (Och)	CD	*Littoridina* (parchapei) sp (Lp)	BDE
Neotrichia sp (Neo)	ACE	*Diplodon chilensis* d'Orbigny (Dc)	D
Diptera		*Glundachia concentrica* d'Orbigny (Gc)	CD

abundance of aquatic vegetation decreased from the positive to the negative end of the axis. Current velocity, substrate size, depth and width decreased from the negative toward the positive end of the axis. The second ordination axis indicated that latitude and water temperature had the next largest effect on the occurrence of species. Thus, warmest temperatures occurred at the negative extreme correlated with low latitudes. Cooler water temperatures at the positive extremes correlated with the position of higher latitudes. Ordination species with regards to the first axes are presented in Figure 3B. Species occurring in high conductivity waters with aquatic vegetation were positioned in the upper right quadrat. Species of fast flowing waters with rocky substrates, with high quantities of wood and leaves occurred in the lower left quadrat. Species occurring in warmer aquatic habitats were positioned in the lower right quadrat.

Species richness and density patterns

Examinations of STATISTICA scatterplots of species richness and macroinvertebrate abundance against environmental variables showed that linear models were appropriate. Total species richness was negatively correlated with latitude and positively correlated with water temperature and altitude, while total density was correlated with conductivity, temperature and altitude (Fig. 4). A subset of independent environmental variables were used in stepwise multiple regression analyses. Altitude and water temperature combined explained only a small part of the variation in species richness ($R = 0.27, n = 29$). Another equation identified latitude depth and FPOM as the strongest predictors of total species richness ($\log(SR+1) = 5.8 - 0.40 \log(L+1) - 0.46 \log(D+1) + 0.33$ FPOM, $R = 0.50$, $P_{lat} < 0.01$, $P_{depth.} < 0.004$, and $p_{FPOM} < 0.04$ $n = 24$). Conductivity and altitude were identified as the most significant predictors of total abundance ($\log(D + 1) = -3.94 + 0.49 \log(C + 1) + 0.48 \log(A + 1)$, $R = 0.45$, $P_{cond} < 0.001$, $P_{altitud.} < 0.002$, $n = 29$). Another significant predictive model also included aquatic plant coverage, altitude and water temperature when the variable conductivity was removed ($\log(D + 1) = -3.47 + 0.43 \log(APC + 1) + 0.42 \log(A+1) + 0.35(\log(T+1)$, $R = 0.55$, $P_{aq.plant cov.} < 0.002$, $P_{altitud.} < 0.003$, $P_{water temp.} < 0.01; n = 29$).

Table 3. Results of canonical correspondence analysis. Total inertia is total variance in species abundance data. The species-environmental correlations scale the strength of the relationship between species and environment for the axes. *F*-ratio statistics are listed for the first axis and for all the axes combined

Axes	1	2	3	4	Total inertia
Eigen values	0.500	0.364	0.289	0.188	
Species-environment correlation	0.973	0.977	0.904	0.919	3.827
Cumulative percentage variance					
of species data	13.1	22.6	30.1	35.1	
of species-environment correlation	22.2	38.4	51.3	59.7	

Test of significance:
Axis1: it F=2.103, *p*<0.005
All canonical axes: *F*=2.247, *p*< 0.005

Discussion

Macroinvertebrate assemblages and environmental relationships

Ordination techniques have been used successfully to interpret macroinvertebrate community structure. In this study, it was possible to describe clear relationships of species-environmental factors. Macroinvertebrates were mainly affected by current speed, water conductivity, substrate size and the abundance of aquatics plant, and secondarily by latitude and water temperature. Similar trends were found in a comprehensive landscape-scale study carried out in Maine (Burian, 1997). Another work carried out in Swedish streams showed that drainage area, alkalinity and water colour were the predominant factors in determining macroinvertebrate assemblages and in that elevation and water temperature were secondary (Malmqvist & Mäki, 1996). Surveys carried out in England showed that pH and total hardness were the main factors explaining benthic community structure, and secondary factors were the slope and stream link magnitude (Ormerod & Edwards, 1987).

Invertebrates such as *Smicridea annulicornis, Klapopteryx kuscheli, Senzilloides panguipulli,* Lumbriculidae sp, *Brachisetodes major* and *Chilenoperla puerilis* seemed to exhibit preferences for fast flowing waters and rocky riverbed, while other species were standing water inhabitants and inhabited sites with high conductivity and rooted aquatic plants. In Australian rivers, there was a significant separation of macroinvertebrate communities from stony or cobble riverbeds and sandy or muddy beds (Marchant & Bar-

muta, 1994). One study showed that enhanced sediment deposition in small high-plain streams influenced macroinvertebrate assemblages (Hubert et al., 1996).

As other studies that have been considering macroinvertebrate longitudinal patterns have shown (Ward, 1986), many members of the mountain stream fauna did not extend into the plain rivers. In this study, *Caenis* sp., *Chironomus* sp., *Rheotanytarsus, Pentaneurini* sp., Syrphidae sp., Tabanidae sp., *Lancetes* sp. and *Diplodon chilensis* were common in the plateau rivers. These faunal discontinuities correspond to the transition from rhithral to potamal conditions, which are expected to occur near sea level at high latitudes (Illies & Botoseananu, 1963).

Meridialaris laminata, *M. chiloeensis, Baetis* sp.1, *Baetis* sp. 3, *Paratrichocladius* sp. 2, *Oxyethira* sp., Elmidae spp. and *Hyalella curvispina* were eurizonal, since they were found in all habitat types described in this survey, although *M. laminata* and *M. chiloensse* were more abundant in running waters than in backwaters. The record of *Righotopus andinensis* in some plateau rivers deserves particular attention because until now it was found only in very clean waters in Los Alerces National Park (Miserendino, 1996). Because of its hard water requirement, *Hyalella curvispina* was mainly observed in high conductivity environments, similar to other studies (Miserendino, 1998).

Invertebrate assemblages in different streams can reflect differences in streamside vegetation (Vannote et al., 1980). Sampling sites in this survey were located in different phytogeographical regions, and their watersheds exhibited distinct types of riparian vegetation. In the CCA ordination, the CPOM fraction was a good limnological predictor of macrozoobenthos com-
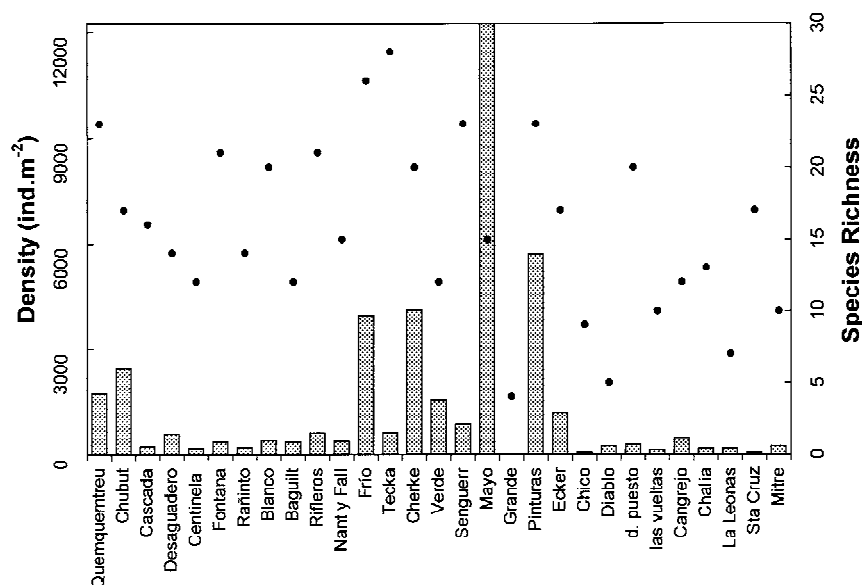
Figure 2. Total species richness (circles) and density (bars) in 29 Patagonian rivers.

position, so rivers characterized by larger quantities of wood and leaves were grouped together in the analyses. These results indicate differences in macroinvertebrate assemblages depending on watershed vegetation. Recent studies have shown that the benthic food web in an Andean freshwater environment is quite distinctive, with a slow rate of decaying organic matter, easily altered by the introduction of exotic tree species (Modenutti et al., 1998). Benthic assemblages in Patagonian running waters seem to be functionally different. In general, fluvial systems maintain multiple interactive pathways across the riverine landscape (Ward, 1998), these features of the water biological resources should be taken into account for management, planning and conservation purposes.

Species richness

Some authors have found that although some few elements are cosmopolitan, most of the Patagonian aquatic animals have a high degree of endemism and remarkable biogeographic differences, which reach the greatest degree in the Plecoptera (Illies, 1969; Wais, 1990). The most species recorded in this survey are endemic.

Biodiversity of stream insects appears to respond to both spatial and temporal variations in physical heterogeneity. However, the degree to which local stream insect assemblages are influenced by regional processes is largely unknown (Vinson & Hawkins, 1998).

Watercourses studied presented an important spatial heterogeneity; they were different in magnitude, water velocity, substrate, aquatic and riparian vegetation and location. In general, latitude and longitude are considered as primary factors to determine species richness of different faunal groups. A study carried out in interior Alaskan streams and rivers showed that several insect orders decreased with increasing latitude (Oswood, 1989). A research conducted in the Negro river basin showed that species richness decreased eastward in the basin from the Andean range streams to the Patagonian Plateau rivers; however, a transitional area of maximum species richness in the middle of both zones was observed (Wais, 1990).

Some authors found that no clear latitudinal gradient has been established for lotic benthic assemblages (Vinson & Hawkins, 1998). Moreover, some relationships have been found between drainage area and species richness (Malmqvist & Mäki, 1996). Despite the low correlation's coefficients, significant values were obtained among species richness and latitude, altitude and water temperature. This study suggests that these factors influence macroinvertebrate richness.

Physically complex substrate types (leaves, gravel or cobble, macrophytes, moss, wood) generally support more taxa than structurally simple substrates (sand and bedrock; Hawkins, 1984; Hubert et al., 1996). Despite the fact that species richness was not correlated with substrate size, gravel-sand substrates
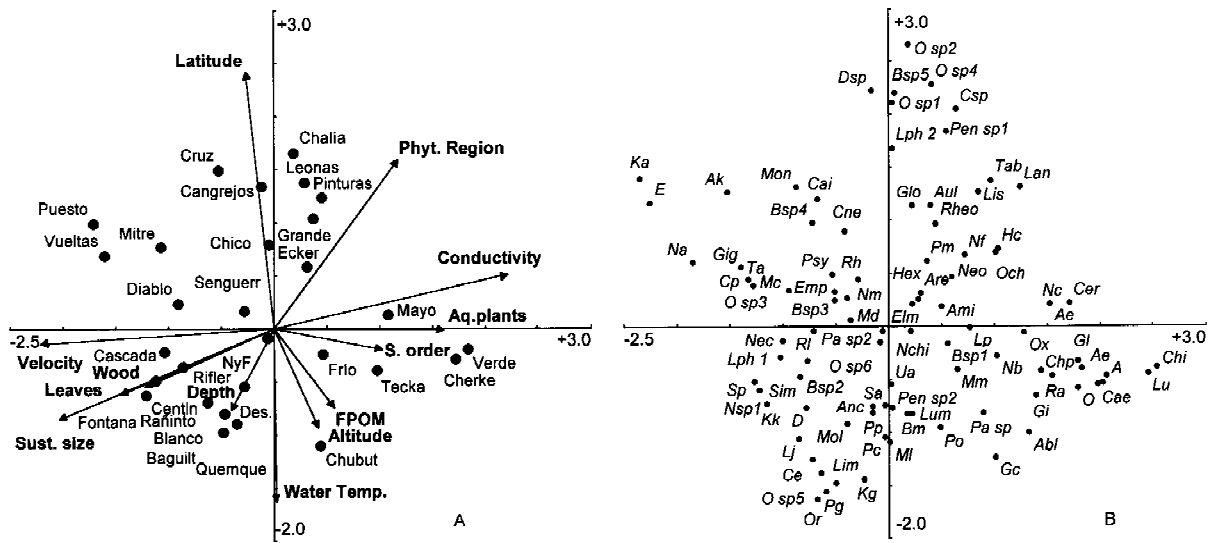
Figure 3. CCA ordination diagrams of macroinvertebrates. (A) Sites-environmental biplot (B) Species-environmental biplot. Full species names can be found in Table 2.
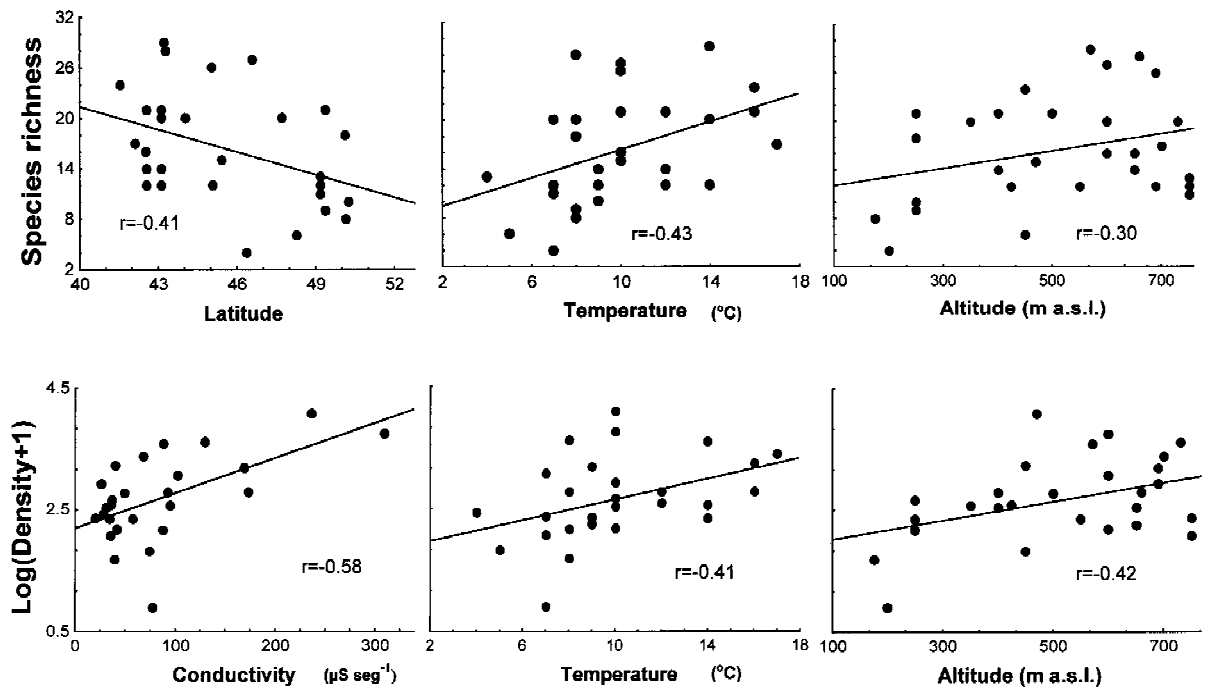

Figure 4. Regression of species richness against latitude, temperature and altitude (top), regression of density against conductivity, temperature and altitude (bottom) ($p < 0.05$ in all cases).

with aquatic plant patches, exhibited more diverse fauna than those consisting of simple sand substrate.

My analyses suggest that both local features and those determined by the landscape affect macroinvertebrate distributions. Habitat heterogeneity was a better predictor of macroinvertebrate assemblages than large-scale patterns in landscape diversity.

Acknowledgements

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