

Habitat type and macroinvertebrate assemblages in low order Patagonian streams

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With 8 figures and 4 tables

Abstract: Benthic macroinvertebrate community structure was studied with respect to stream habitat type in four low-order Patagonian streams (Argentina). Seven habitat types were sampled during high and low water periods in each river. Boulders, cobbles, pebbles and gravels were sampled in run/riffle sections, whereas sand, leaf packs and macrophytes were sampled in pools. Run-riffles supported higher densities and biomasses of invertebrates than sand in pools but had densities similar to those in macrophytes. Benthic organic matter was highest in leaf packs in pools (4.21 g DM/0.1 m²) and was composed of leaf fragments, wood and entire leaves. The dry weight of organic matter among boulders, cobbles and pebbles in riffles areas ranged from 0.69 to 0.85 g DM/0.1 m². Detrended correspondence analysis showed that species assemblages differed seasonally, and that species associations differed markedly among substrata and rivers. Proportions of five functional feeding groups differed among habitats, although gatherers were dominant in most habitat types. Shredders and collector-gatherers co-dominated numerically in leaf packs but shredder biomass was highest among boulders and gravels. Filterers were numerically dominant on macrophytes and gravels, whereas scrapers were common on all riffle substrata. At the habitat scale, current velocity, water temperature and organic matter availability appear to be major factors affecting the distribution and abundance of Patagonian stream invertebrates. Our results provide baseline data on poorly studied river systems whose integrity is threatened by sediment inputs from forestry and agriculture.

Key words: Organic matter, macroinvertebrates, species assemblages, functional feeding groups, Patagonia.

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Introduction

The physical habitat of stream biota is a spatially and temporally dynamic entity determined by the interaction of structural features of the channel and the hydrological regime (MADDOCK 1999). A stream may be viewed as a mosaic of patches characterized by different environmental conditions (PRINGLE et al. 1988) in which the distribution of benthic macroinvertebrates reflects the distribution of benthic resources. Since variation in benthic community structure can be explained at the level of habitat type, several authors have quantified habitat units in rivers as well as distribution of benthic resources (WOHL et al. 1995, ANGRADI 1996). In low order streams, "pools" are depositional habitats in which fine sediments accumulate during low water periods, whereas "run/riffles" are erosional habitats, from which small particles are exported (CUMMINS 1972). The nature of the benthic organic matter trapped among different hard substrata (gravel vs. boulder) in riffles can determine variation in macroinvertebrate abundance (PARKER 1989). Some authors have found that run/riffles in mountain rivers support higher diversity and species richness than depositional zones (HYNES 1970, BUFFAGNI & COMIN 2000). However, leaf packs in run/riffles can also have high invertebrate diversity and abundance (RAMÍREZ & PRINGLE 1998).

Habitat heterogeneity, defined on the basis of availability of resources (food, refuges) at diverse spatial scales, is one of the most important features determining the distribution of species (FRISELL et al. 1986, VINSON & HAWKINS 1998, BIS et al. 2000). In lowland streams, species richness typically increases on aquatic plants, which contribute a greater amount of habitat (ARMITAGE et al. 1995). In low order streams, species richness is higher on stable substrata such as cobbles and within leaf packs in riffles (MARCHANT 1988, MARCHANT & BARMUTA 1994, MOOG & JANECEK 1991).

River management practices and anthropogenic stress can affect ecological processes at the habitat scale in several ways. For example, they result in increases in sediment deposition, alterations in streamflow, and changes in the nature of benthic organic matter (HUBERT et al. 1996, BARBOUR et al. 1999). Changes in stream benthos resulting from the manipulation or disturbance of rivers have been documented for Patagonian mountain streams (MISERENDINO & PIZZOLÓN 1999, 2000). Benthic assemblages of invertebrates, and patterns of distributions along an altitudinal gradient have also been described (WAIS 1987, ALBARIÑO 1997). However, there appear to be no studies of benthos in relation to habitat types, which might reveal potential consequences of habitat manipulation as a result of recent land development in the area. Forestry practices, conversion to pasture, fisheries, and mining are activities that are increasing rapidly in the northwest of Patagonia.

The main goals of the study were 1) to assess whether particular macroinvertebrate species assemblages are associated with particular habitat types, and 2) to examine functional organization and benthic matter storage at the habitat scale in low-order streams in Patagonia.

Study area

The study was conducted in four rivers in northwestern Patagonia ($43^{\circ} 12' S$; $71^{\circ} 31' W$). The present landscape is strongly influenced by glacial action and strong fluvial erosion, and is characterized by steep slopes, narrow valleys and high rainfall. Catchments are dominated by granites and diorite rocks. Extensive outcrops of crystalline bedrock produce ionically dilute waters, a distinctive characteristic of the Andean-Patagonian Cordillera region (DRAGO & QUIRÓS 1996). All four studied streams are 2nd (Blanco) or 3rd (Baggilt, Rifleros and Nant y Fall) order tributaries of the Futaleufú River (Fig. 1).

Mean annual conductivity of river water at the study sites ranged from 17 to $90 \mu S_{20} cm^{-1}$, whereas alkalinity ranged from 0.5 to $1.38 meq l^{-1}$ (MISERENDINO & PIZZOLÓN 1996). Streamflow in the region is strongly linked to precipitation and snow-

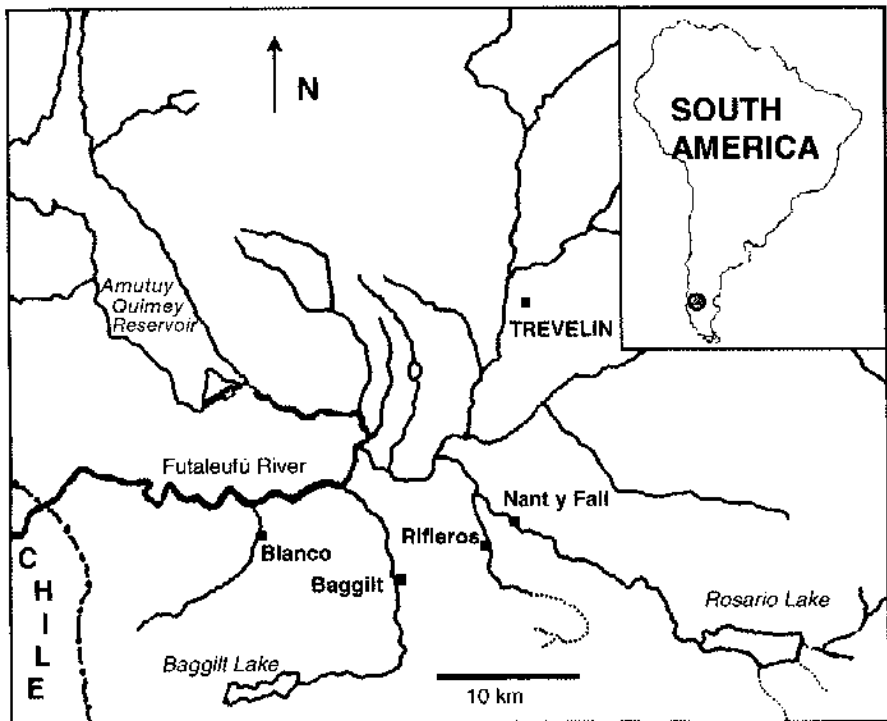


Fig. 1. Study area showing the location of sampling sites.

melt, which result in winter and spring spates. However, during summer, river flow is low and stable (CORONATO & DEL VALLE 1988). The Blanco and Baggilt River watersheds are covered by native deciduous forest dominated by *Nothofagus pumilio* (POEPP. et ENDEL.) KRASEN, and the perennial cypress *Austrocedrus chilensis* (D. DON). The latter is also common in the high forest of the Rifleros watershed. The low basin of the Rifleros River, and the Nant y Fall basin downstream of Rosario Lake (Fig. 1), are covered by deciduous *Nothofagus antarctica* (FORST. F.) OERST forest, but at the study sites native riparian vegetation has been replaced by introduced willow *Salix fragilis* L. Willows and grasses also dominated the riparian zone at the Rifleros and Nant y Fall study sites, whereas native forest bordered the Blanco and Baggilt Rivers.

Materials and methods

Sampling design

Sampling was undertaken during high (November 1999) and low water periods (March 2000). Each of the rivers (Blanco, Baggilt, Rifleros, Nant y Fall) was visited twice. The selected sites were at comparable elevation (350–400 m a.s.l.). In depositional areas (pools) three habitat types were sampled: sand (S), leaf pack (LP) and macrophytes (M). In run-riffle areas four different habitats were sampled: boulder (B), cobble (C), pebble (P) and gravel (G). The relative proportion of each habitat type was assessed using a grid, as described by RAMÍREZ et al. (1998). The dimensions of the grid were 4 m × river width, with the grid being divided into 16 equal sections. The percentage of all habitats occupying each section of the grid at each site was estimated.

At each site, water and air temperature were measured with a thermometer, during the morning. Current speed was estimated by timing a bobber (average of 3 times) as it moved over a distance of 10 metres (GORDON et al. 1994). Average depth of the reach was calculated from three measurements taken at equal intervals across the channel with a calibrated stick. Wet and dry widths of the streambed were measured as in BARBOUR et al. (1999).

Three Surber samples (0.1 m^{-2} , 250 μm pore size) were taken from each habitat in each stream, during the dry and wet seasons, for a total of 78 samples. Samples were fixed with formaldehyde in the field and were sorted and preserved in 70% ethanol in the laboratory. Sorting involved elutriation and the collection of materials on a series of sieves (mesh width 250 μm –1000 μm). Detritus was divided into fine (250 μm –1000 μm) and coarse (>1000 μm) particulate fractions (FPOM and CPOM, respectively). CPOM was separated into wood, leaves (mainly entire leaves) and others (fragments of leaves, grass, seeds, roots, buds, etc) (VOELZ & WARD 1990). All fractions were dried (105 °C for 24 h) and weighed on an electronic balance to $\pm 0.5 \text{ mg}$.

All organisms were identified to the lowest taxonomic level possible using available keys (ANGRISANO 1995, ANGRISANO & TREMOUILLES 1995, BENEDETTO 1974, DOMÍNGUEZ et al. 1994, BACHMANN 1995). Density was calculated from counts of all the individuals in a sample, whereas biomass was estimated using length-mass relationships as in MISERENDINO (2001a). Functional feeding groups were assigned by gut

analyses and using available references (MERRITT & CUMMINS 1978, DOMÍNGUEZ et al. 1994, ALBARIÑO & BALSEIRO 1998).

Statistical analyses

Fixed-effects 3-factor ANOVA models were used to assess significant differences in species richness, total density, total biomass and benthic organic matter (dry mass) between habitats (7), streams (4) and dates (2). The interaction between stream and season, and habitat and season were also assessed. A posteriori comparisons among habitats were performed with Tukey's (HSD) test ($p < 0.05$).

To investigate macroinvertebrate distribution per habitat, Detrended Correspondence Analysis (DCA: an eigen analysis ordination technique based on reciprocal averaging; HILL & GAUCH 1980) was performed for each river, separately, using the PC-ORD statistical package (version 3.0, McCUNE & MEFFORD 1997). Log ($x+1$) transformed species abundance data were used. Cluster analysis was also carried out on log ($x+1$) transformed abundance data and on percentage occurrence data for all species within a habitat and with seasons combined (LUDWIG & REYNOLDS 1988). Clustering was performed with Ward's linkage and the one minus Pearson correlation distance (dissimilarity) measure, (McGARIGAL et al. 2000), using the Statistica package.

To explore species-environmental relationships in habitats at all river sites, a Canonical correspondence analysis (CCA) was performed using CANOCO version 4.3 (TER BRAAK & SMILAUER 1998). This multivariate, direct gradient analysis enables non-linear species abundance data to be analyzed along with linear environmental data (TER BRAAK 1986). Two environmental variables, altitude and dry river width, were omitted because multicollinearity was indicated by a large variance inflation factor (>20) (TER BRAAK & SMILAUER 1998, 1999). In CCA biplots the first and the second axes represent the most important environmental gradients along which species and samples are distributed. The significance of relationships on this pair of axes was tested using a Monte Carlo Test (999 permutations) (JCKEL 1986).

Results

Physical features and particulate organic matter

Habitat proportions differed among the study sites (Table 1). In Blanco River, boulders in riffles were most abundant, whereas in Baggilt cobbles and pebbles were the dominant substrata. At the Rifleros River site, sand made up 31.25 % of the substrata. Macrophytes were mainly recorded at Nant y Fall, where the most abundant species was *Myriophyllum* sp. Temperature was lower in the wet than dry season, and current speed was approximately twice as high in the wet season at all sites except Nant y Fall where differences were not so marked.

Biomass of benthic organic matter differed among streams and habitat types (Table 1, Fig. 2), and was highest in the Baggilt River. The fraction

Table 1. Physical characteristics, percentage of substrate types and mean total values of fine (FPOM) and coarse organic matter (CPOM) per sample (0.1 m²) measured during high and low water periods.

	Blanco		Baggilt		Los Rifleros		Nant y Fall	
	High	Low	High	Low	High	Low	High	Low
Width (wet) of the stream (m)	21	13.20	9.5	7	9	7	11.5	9
Width (dry) of the stream (m)	23	14.20	13	12	12.5	10.5	15	12
Water Temperature (°C)	5	11	7	12.5	8	14.5	9	11
Current speed (cm·s ⁻¹)	56	25	81	46	85	38	86	79
Riffles								
Boulder (%)	50		0		25		0	
Cobble (%)	31.25		25		25		0	
Pebble (%)	18.75		43.75		18.75		31.25	
Gravel (%)	0		0		0		37.50	
Pools								
Sand (%)	0		0		31.25		0	
Leaf-pack (%)	0		31.25		0		0	
Macrophytes (%)	0		0		0		31.25	
FPOM								
(g DM/0.1 m ²)	0		1.74		0.33		1.13	
CPOM								
Leaves (g DM/0.1 m ²)	1.34		6.23		0.84		1.05	
Wood (g DM/0.1 m ²)	1.64		11.71		0.83		0.36	
Others (g DM/0.1 m ²)	5.51		21.51		13.14		12.64	

Table 2. Mean total dry mass of organic matter by habitat type (g DM 0.1 m⁻²) and percentage composition (in parentheses) of each detrital category at all sites combined.

	Riffle				Pool	
	Boulder	Cobble	Pebble	Gravel	Leaf-packs	Sand
FPOM	0.09 (1)	0.02 (2)	0.01 (1)	0.19 (11)	0.23 (6)	0
Other	0.53 (69)	0.49 (62)	0.46 (57)	1.48 (86)	2.21 (52)	0.72 (100)
Wood	0.14 (19)	0.15 (20)	0.14 (17)	0	1.12 (26)	0
Leaves	0.09 (11)	0.12 (15)	0.08 (25)	0.04 (2)	0.65 (15)	0
Mean total benthic organic matter	0.85	0.79	0.70	1.71	4.21	0.72

“others” dominated in most habitats, especially among gravel and boulders in riffles and leaf packs in pools (Table 2). The percentage of wood was similar on boulder, cobble, and pebble substrata, but more wood was associated with leaf packs. Leaf packs and gravels had higher contributions of FPOM (6% and 11%, respectively) than the other habitats. In most habitat types the FPOM fraction was higher in spring (high water period) than summer (low water pe-

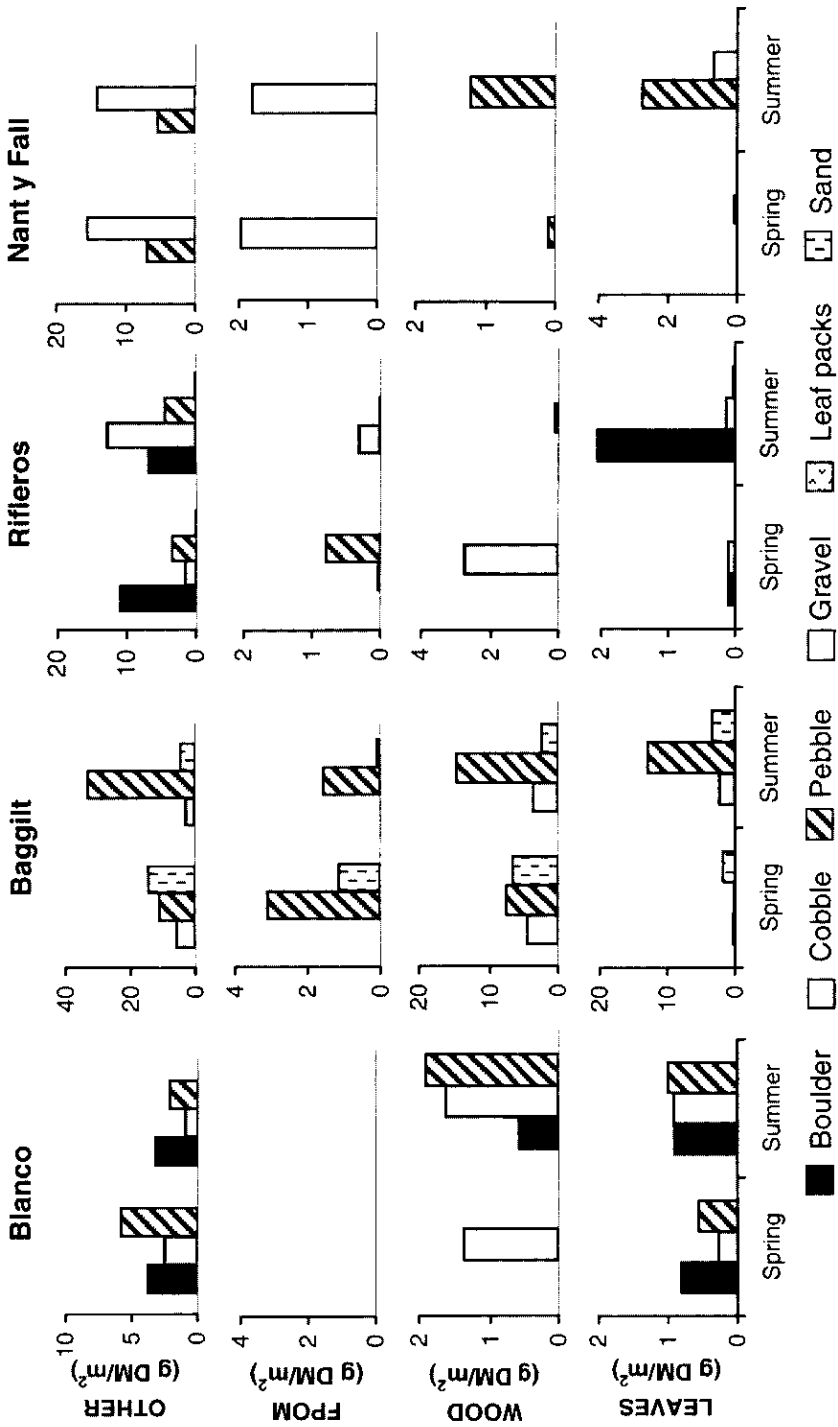


Fig. 2. Inter-habitat and seasonal variation in mean total values (g DM/m²) of 4 organic matter categories (n = 3). Note the scales on the y-axes differ among streams.

riod) (Fig. 2). Conversely, more leaves were present in summer than spring (Fig. 2, Table 3). Leaf fall in the deciduous *Nothofagus pumilio* and *Salix fragilis* occurred in autumn and coincided with the first high discharge peak.

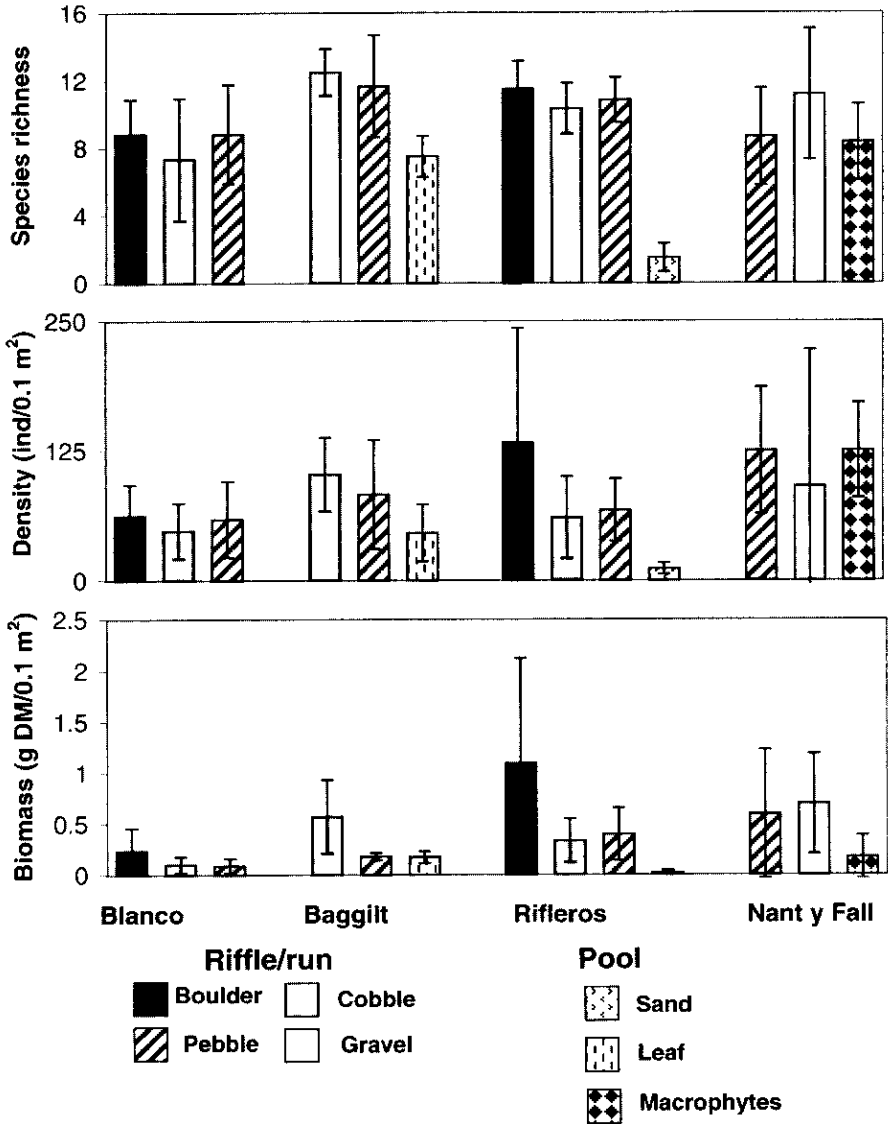


Fig. 3. Inter-habitat variation in mean (± 1 SE) species richness (top), density (middle) and biomass (bottom) ($n = 6$), for each stream.

Effect of habitat type on macroinvertebrates

Mean species richness per sample was highest in riffles. Boulders supported most species at the Blanco and Rifleros sites, cobbles in the Baggilt and gravel in Nant y Fall, however, values were not significantly different among coarse substrata at individual sites (Fig. 3). Sand in pools had significantly lower species richness than the other habitats (ANOVA, $P < 0.005$) (Tables 3 and 4).

Mean abundance per unit area showed differences among substratum types (Fig. 3). Pools containing sand had significantly lower densities of invertebrates than the other habitats (ANOVA, $P < 0.005$), and leaf packs had lower densities than macrophytes, although the difference was not significant ($P > 0.05$, Table 4). Boulders and gravel in riffles had high mean macroinvertebrate biomass, and sand supported the lowest biomass (Fig. 3, Table 3). Seasonal differences were observed in total biomass (ANOVA, $F = 3.9$, $P < 0.05$; Table 3), which was higher in spring than summer.

Except for the sand habitat in the Rifleros River, all habitats had different assemblages of invertebrates during the high and low water periods (Fig. 4). Thus, DCA axis 1 in Blanco, Baggilt and Nant y Fall, and DCA axis 2 in Rifleros, showed a clear separation among habitats sampled during high and low water periods. Moreover, coarse substrata (B, C, P) were separated from organic substrata along DCA axis 2 in Baggilt, although the separation between macrophytes, cobbles and gravels was less clear in Nant y Fall. At Nant y Fall Gr and M were identified as separate groups only during the low water period.

The macroinvertebrate assemblages in each habitat type are shown in Table 4. Only five taxa were associated with one habitat type more than 80% of the times, *Hexatoma* sp. (Tipulidae) with macrophytes, *Meridialaris laminata* (Leptophlebiidae), Lumbriculidae sp2, *Chilina patagonica* (Gasteropoda), and Lumbriculidae sp1 with sand. However, 15 species were associated with one or two substratum types more than 49% of the time. They included *Paraseri-*

Table 3. Results of three-way ANOVAs examining the effects of habitat type, stream and season on total density, biomass, species richness and fractions of benthic organic matter. Variables log (x + 1) transformed. * = $p < 0.05$, ** = $p < 0.005$.

	Habitat $F_{(6,52)}$	Stream $F_{(3,52)}$	Season $F_{(1,52)}$	Stream × Season $F_{(3,52)}$	Season × Habitat $F_{(6,52)}$
Species richness	27.8**	6.2**	0.06	2.24	1.15
Total density	7.07**	4.5*	1.86	1.10	1.21
Total Biomass	4.6**	4*	3.92*	0.03	1.79
FPOM	7.3**	3.74*	1.21	0.58	0.37
Leaves	8.87**	14.26**	26.29**	6.8**	7.7**
Wood	4.74**	9.77**	0.02	0.39	0.24
Other	11.39**	11.46**	0.02	1	4.04**

Table 4. Mean abundance of macroinvertebrates (ind. 0.1 m⁻²) and percentage occurrence (in parentheses) of 36 taxa in different habitat types in low order streams in Patagonia. Taxa are assigned according to their abundance values (higher to lower) in all habitats combined. Taxonomic group: G: Gripopterygidae, P: Perlidae, A: Austroperlidae, B: Baetidae, L: Leptophlebiidae, Am: Ameletopsidae, S: Sericostomatidae, H: Hydrobiosidae, Hp: Hydropsychidae, Lp: Leptoceridae, C: Chironomidae, T: Tipulidae, At: Athericidae, Si: Simuliidae, E: Elmidae, Hy: Hyalellidae, Ch: Chilinidae, and Lu: Lumbriculidae. L: list of taxa codes used in the CCA analysis. Functional feeding groups (FFGs) assigned: S, shredder; P, predator; Sc, scraper; CG, collector-gatherer, and CF, collector-filterer. Numbers with the same subscript are not different in ANOVA test ($P < 0.005$).

Tax. Group	Taxa	L	FFG	Boulder	Cobble	Pebble	Gravel	Macroph.	Sand	Leaf packs
S	<i>Parasericostoma ovale</i> SCHMID	Po	S	1.5 (50)	4.5 (33)	3.4 (39)	12.2 (67)	0.33 (33)	0.5 (33)	0.8 (33)
Hp	<i>Smicridea annulicornis</i> BLANCHARD	Sm	F	13.7 (50)	4.8 (50)	5.2 (56)	1.8 (67)	1.5 (67)		
G	<i>Chilenoperla puerilis</i> ILLIES	Cp	S	6 (42)	1.1 (21)	2.9 (11)				
G	<i>Sencilloides pungaipulli</i> NAVÁS	Sp	S	1.2 (17)		0.8 (5)				
B	<i>Baetis</i> sp. 2	B2	CG	2 (42)	0.6 (33)	1 (44)	0.16 (17)	0.16 (17)		
B	<i>Baetis</i> sp. 3	B3	CG	1.7 (25)	1 (38)	0.9 (28)				
G	<i>Rhithroperla rossi</i> FROELICH	R	Sc	0.2 (8)						
E	<i>Austrelmis</i> sp.	Au	Sc	2.5 (50)	2.7 (54)	2.6 (66)	0.3 (16)	0.33 (33)		2.17 (66)
G	<i>Aubertoperla illiesi</i> ILLIES	Ai	Sc	1.7 (33)	2 (29)	1.7 (28)		0.2 (17)		0.2 (17)
P	<i>Pictoperla gayi</i> PICTET	Pg	P		1 (21)	0.1 (11)				
Am	<i>Chiloporter eatoni</i> LESTAGE	Ce	P	0.2 (17)	0.9 (8)	0.2 (22)				
A	<i>Klapopteryx kuscheli</i> ILLIES	Kk	S		0.5 (21)	0.2 (17)				
G	<i>Pelargoperla personata</i> ILLIES	Pp	CG	0.1 (8)	0.2 (8)	0.1 (11)				
Lp	<i>Nectopsyche unispina</i> FLIN F	Nu	S			0.5 (5)	0.2 (33)			
H	<i>Araucanioperla hulocki</i> NAVÁS	Ab	Sc		0.3 (13)	0.2 (11)				
H	<i>Rheochorema</i> sp.	Rs	P		0.1 (4)					
L	<i>Meridialaris chiloeensis</i> (DEMOULIN)	Mc	CG	1.1 (33)	3.7 (29)	13.1 (28)				
G	<i>Limnoperla joffueli</i> NAVÁS	Lj	Sc	0.5 (17)	0.8 (13)	4.3 (33)				1.2 (17)
G	<i>Notoperlopsis femina</i> ILLIES	Nf	Sc	0.2 (8)	0.4 (21)	1.3 (28)			0.3 (17)	1.2 (33)
G	<i>Antarctoperla</i> sp.	A	S		0.2 (17)					
L	<i>Meridialaris diguillina</i> ULMER	Md	CG	2.3 (25)	3.3 (46)	4.6 (31)				0.8 (33)
C	<i>Parochlus</i> sp.	Par	CG	1.5 (42)	2 (33)	1.3 (22)	0.5 (22)	4.8 (17)		1.3 (33)
C	<i>Paratrichocladius</i> sp.	P	CG	9.9 (83)	9.8 (83)	5.9 (66)	19 (67)	31 (67)		13.8 (67)
T	<i>Hexatoma (Eriocera)</i> sp.	H	P	2.5 (25)	6.8 (33)	0.6 (16)	3.5 (50)	27.7 (83)		
C	<i>Ablabesmyia</i> sp.	Abl	CG	3.08 (33)	0.7 (21)	0.5 (22)		2.7 (50)		
Hy	<i>Hyallela curvispina</i> SHOEMAKER	Hc	CG					0.7 (33)		
Si	<i>Simulium</i> sp.	Si	CF	14.3 (50)	4.75 (29)	7.3 (33)	56.8 (33)	43.8 (33)		0.8 (33)
L	<i>Meridialaris laminata</i> (ULMER)	Ml	CG	5.6 (50)	6.5 (42)	4.7 (39)	12.3 (83)	0.3 (33)		
Lu	<i>Lumbriculidae</i> sp. 2	Lu2	CG	1.3 (25)	3.2 (38)	1.4 (22)	5 (83)	2.7 (67)	0.3 (17)	2.8 (33)
Ch	<i>Chilina patagonica</i> SOWERBY	Cpa	Sc	1.6 (42)	1 (42)	0.6 (42)	1.7 (83)	0.8 (50)	0.5 (17)	0.3 (17)
Lu	<i>Lumbriculidae</i> sp. 1	Lu1	CG	0.5 (8)	1.7 (21)	0.2 (11)	3 (17)	1.2 (17)	9.8 (83)	0.5 (17)
Lp	<i>Brachysetodes major</i> SCHMID	Bm	S	5.6 (50)	6.7 (67)	3.1 (55)	4.3 (100)	4.3 (67)	9.2 (83)	
L	<i>Penaphlebia chilensis</i> (EATON)	Pch	CG	0.2 (8)	1.2 (29)		0.3 (17)	0.8 (33)		4.2 (33)
1.	<i>Nousia bella</i> PESCADOR & PEETERS	Nb	CG	0.1 (8)	0.4 (17)	0.3 (22)	3.3 (50)	0.8 (50)		3.5 (67)
B	<i>Baetis</i> sp. 1	B1	CG	1 (17)	1.7 (33)	0.66 (39)	0.6 (33)	0.3 (33)		1.7 (50)
At	<i>Dasyoma</i> sp.	D	P	1.5 (58)	1.2 (46)	1.5 (50)				1 (50)
	Total species richness			29	31	32	17	20	4	17
	Mean species richness			10 ^a	10 ^a	10 ^a	8 ^a	9 ^a	1 b	7 ^a
	Mean total abundance (ind. 0.1 m ⁻²)			97 ^a	73 ^a	73 ^a	125 ^a	125 ^a	11 ^b	45 ^a
	Mean total biomass (g. DM 0.1 m ⁻²)			0.66 ^a	0.33 ^{ab}	0.31 ^{ab}	0.70 ^a	0.17 ^{ab}	0.02 ^b	0.17 ^{ab}

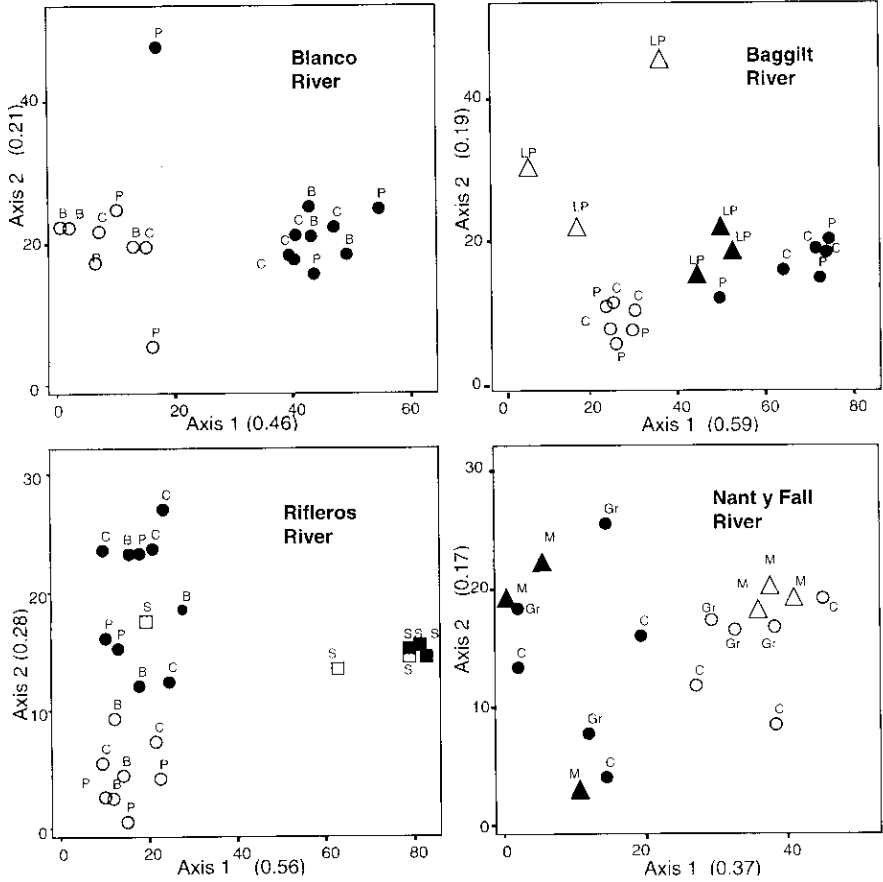


Fig. 4. Ordination of habitat types sampled in four streams in the Patagonian mountains using Detrended Community Analysis. Symbol codes as follows: Circles: large inorganic particles, Squares: sand, Triangles: organic substrata. Open symbols: low water period, filled symbols: high water period. B: boulder, C: cobble, P: pebble, Gr: gravel, S: sand, LP: leaf packs, M: macrophytes.

costoma ovale (Sericostomatidae), *Smicridea annulicornis* (Hydropsychidae), *Austrelmis* sp. (Elmidae), *Paratrichocladius* sp. (Chironomidae), and *Dasyoma* sp. (Athericidae). The taxon with the highest occurrence in sand was a species of Lumbriculidae, whereas on macrophytes *Hexatoma* sp. was most abundant. Several species were held in common by macrophytes and gravel: *Hexatoma* sp., Lumbriculidae sp2, *Hyallega curvispina* (Amphipoda), *Ablabesmya* sp. (Chironomidae), *Chilina patagonica* and *Meridialaris laminata*.

In leaf packs, three mayflies species (*Nousia bella*, *Baetis* sp1 and *Penaphlebia chilensis*) had the highest occurrences (Table 4). The main assemblages in the boulder-cobble-pebble habitat were the stoneflies *Chilenoperla puerilis*

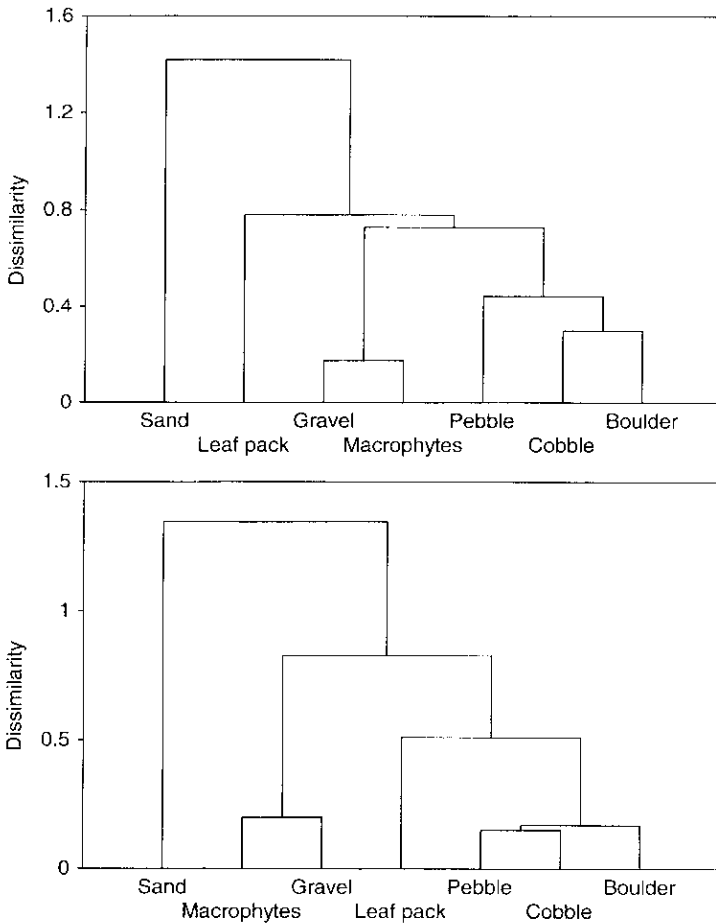


Fig. 5. Cluster analyses (r -Pearson, Ward linkage method) based on abundance (top) and percentage occurrence (bottom) dissimilarity of macroinvertebrates per habitat type in all studied sites combined.

and *Aubertoperla illiesi*, and the mayflies *Meridialaris chiloeensis*, *Baetis* sp2 and *Baetis* sp3.

Cluster analyses, based on both mean abundance and percentage occurrence of taxa, showed that boulders, cobbles and pebbles had similar assemblages. Furthermore, gravel and macrophyte assemblages were grouped together (Fig. 5), consistent with the DCA results.

Functional feeding groups

Collector-gatherers, mostly chironomids and leptophlebiids, had the highest densities in practically all habitat types, an exception being in gravels where

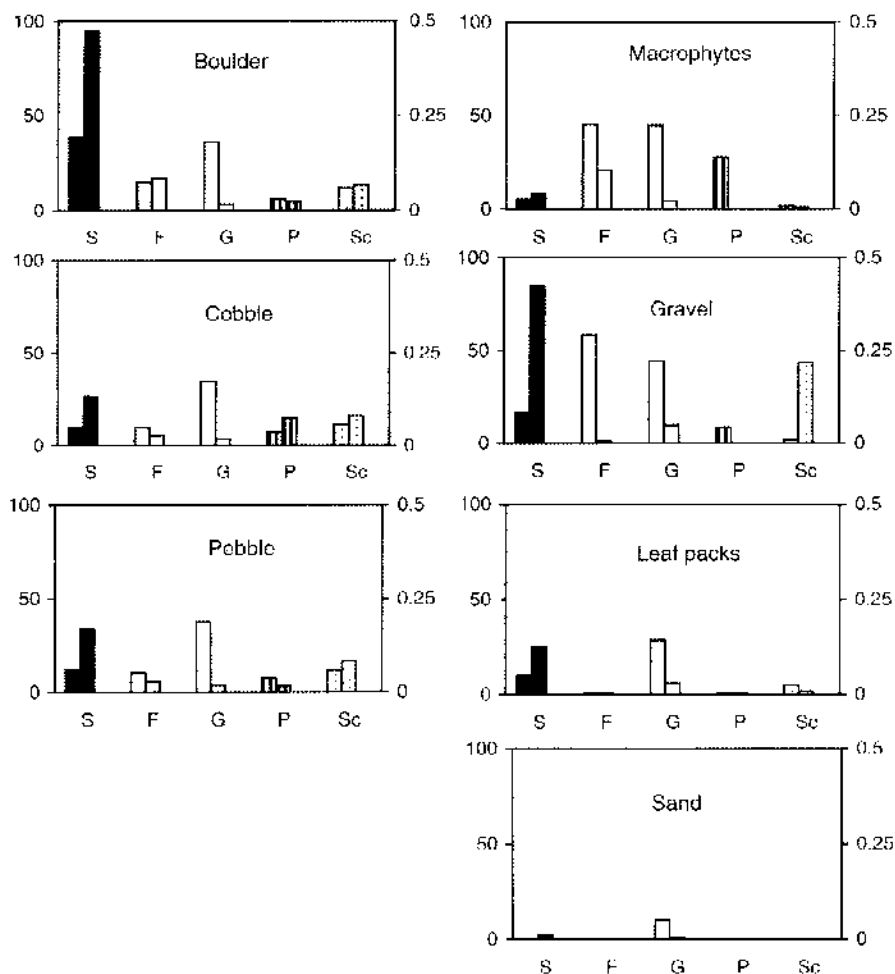


Fig. 6. Mean total density (ind/0.1 m², left bar) and biomass (mg/0.1 m², right bar) of functional feeding groups of macroinvertebrates per habitat type at the study sites. S: shredders, F: filterers, G: gatherers, P: predators, Sc: scrapers.

the filterers *Smicridea annulicornis* and *Simulium* sp. were dominants (Table 4, Fig. 6). Shredders had the highest biomass at most sites, except on macrophytes where filterers had the highest biomass. Shredder density was high on boulders, but low among pebbles and cobbles, and in leaf packs. The most common shredders were *Brachysetodes major*, *Klapopteryx kuscheli* and *Parasericostoma ovale*. The highest density of predators occurred on macrophytes where *Hexatoma* sp. was common. However, the highest biomass of predators was on cobbles where the large larvae of *Pictetoperla gayi* (Plecoptera) and *Chiloporter eatoni* (Ephemeroptera) were found (Fig. 6). Scrapers

had high biomass on cobbles, pebbles and gravels, where the most common scraper taxa were *Austrelmis* sp., *Linnoperla jaffueli*, and *Chilina patagonica*.

Environmental relationships

Stream wet width, current velocity, water temperature, depth and wood biomass were the main environmental variables correlated with CCA axes, indi-

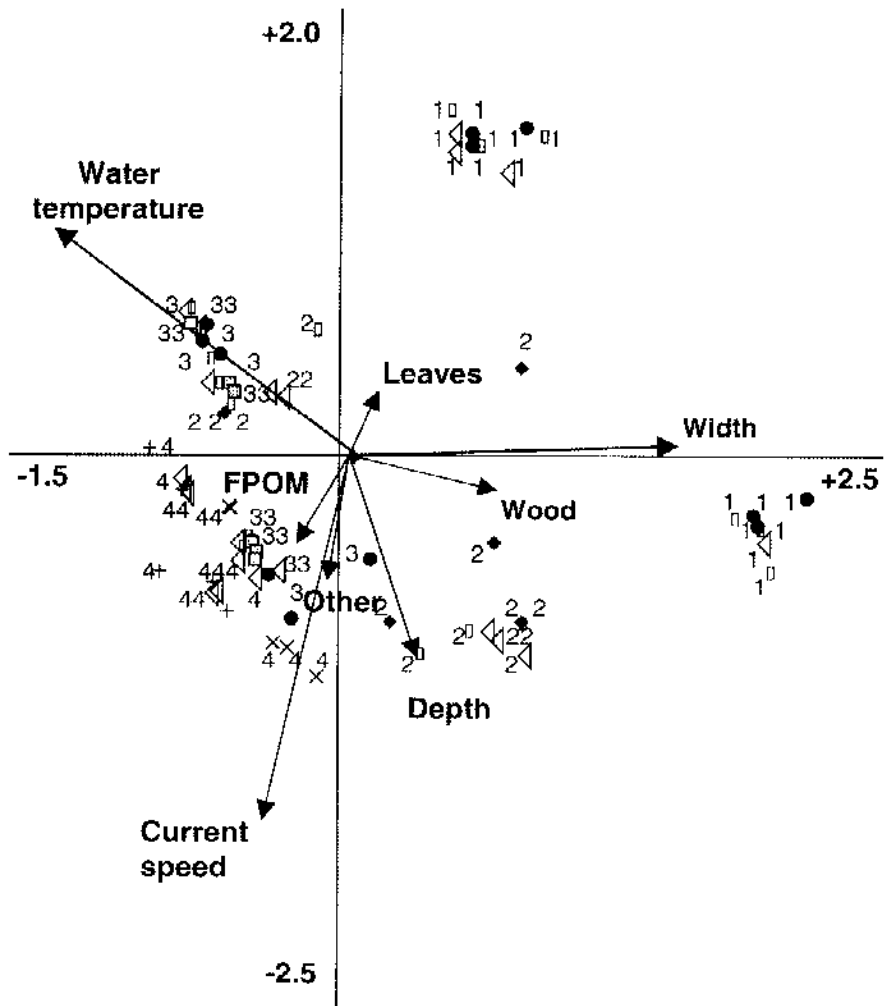


Fig. 7. Canonical correspondence analysis ordination plot for sites and environmental variables. Code for streams: 1: Blanco, 2: Baggilt, 3: Rifleros and 4: Nant y Fall. Code of habitat types: ●: boulders, ■: sand, ◆: leaf packs, □: pebbles, △: cobbles, X: macrophytes and +: gravel.

cating that predictors of macroinvertebrate assemblages at the habitat scale were associated with the size of the reach, but also were affected by variables that changed, seasonally. The ordination obtained was tested by the Monte-carlo test (for the first axis $F = 7.687$ and $P < 0.005$ all the axes: $F = 3.358$ and $P < 0.005$) meaning that canonical axes extracted were significant. Species-environmental factor correlations were $CCA1 = 0.89$ and $CCA2 = 0.88$, indicating high correlation of the environmental variables selected. The CCA indicated stronger relationships among habitats within a river, than among similar

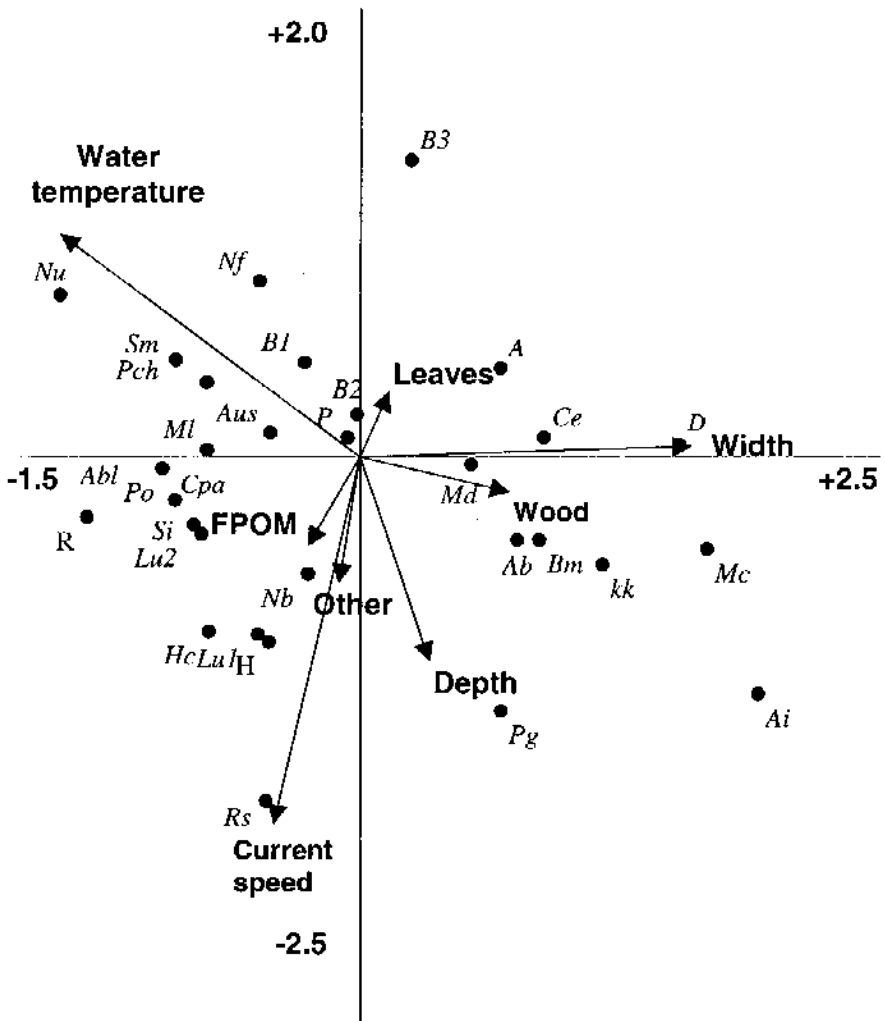


Fig. 8. Canonical correspondence analysis ordination plot for species and environmental variables. Code of species in Table 4.

habitat types in different rivers. Thus, samples from a particular river clustered together in the biplot (Fig. 7). Habitats sampled during low water period were positioned in both the left and right upper quadrants. Conversely, habitats sampled during high water period were located only in the lower quadrants, meaning that discharge probably affected habitat persistence and also benthic organic resources. During spring, the fraction 'other' and FPOM increased. Species recorded during the low water period were positioned in both the left and right upper quadrants, while those recorded in the wet season were positioned in the lower quadrants (Fig. 8).

Discussion

Macroinvertebrate assemblages exhibited differences in species richness, density, and biomass among substrata and habitat types in the rivers studied. Stony substrata in riffles supported higher density and biomass of macroinvertebrates than sand and leaf packs in depositional areas, in both dry and wet seasons. These results are consistent with those observed for other low-order rivers in mountain areas (LYNES 1970, BROWN & BRUSOCK 1991), and contrast the observations of ANGRADI (1996) who found that debris pools supported higher densities of invertebrates than riffles in headwaters Appalachian streams. Leaf packs and pebbles in riffles often support a high density and biomass of macroinvertebrates (RAMÍREZ & PRINGLE 1998, WHITLEDGE & RABENI 2000). Although leaf packs were not *a priori* identified as entities in riffles in our study, considerable amounts of coarse organic matter including entire and fragmented leaves were associated with boulders and cobbles in these areas.

Some authors have found that pools or depositional habitats in tropical areas have lower density and biomass of macroinvertebrates than other habitat types, because they are subjected to greater predation and physical disturbance (BROWN & BRUSOCK 1991, PRINGLE 1996). In our study, riffles had more taxa and supported a greater density of invertebrates than sand or leaf packs in pools, probably because the latter depositional environments were unstable (dominated by sand) and disturbed by increases in discharge. In contrast, the macrophyte *Myriophyllum* supported a similar density of invertebrates in depositional area (pools) as did boulders and cobbles, suggesting it provides a stable substratum and feeding site.

GILLER & MALMQVIST (1998) postulated that most benthic taxa are substratum generalists, although many may show a degree of preference for broad substratum categories. However, despite weak substratum specificity there are some taxa that do occur only on particular substrata (ALLAN 1995). In the pre-

sent study, *Klapopteryx kuscheli*, *Pictetoperla gayi* and *Araucanioperla bullocki* fell into this category, as they were found only on cobbles and pebbles. We also found particular assemblages of species on large substrata in riffles (boulders, pebbles, cobbles), gravels in riffles, and macrophytes, sand, and leaf packs in pools. Thus, specific habitat preferences seemed to be related principally to the category (organic-inorganic), and stability (stable-unstable) of the substratum. When we analyzed preferences for substratum size within the coarse category (boulder, cobble and pebble), differences were not so marked, but assemblages were still different from those on gravel and sand. These findings are consistent with those of previous Patagonian studies, which have indicated that inorganic substratum size was a good predictor of stonefly assemblages (MISERENDINO 2000), and some taxonomically more diverse macroinvertebrate assemblages at a landscape scale (MISERENDINO 2001 b), and along altitudinal gradients (MISERENDINO & PIZZOLON 2000). WINTERBOURN & GREGSON (1989) indicated that many stream invertebrates in New Zealand have substratum preferences; many of these are related to endemic Patagonian taxa (e.g. Austroperlidae, Notonemouridae, Armeletopsidae). Furthermore, QUINN & HICKEY (1990) found that taxonomic richness and density in New Zealand streams were highest on small cobbles, large cobbles and boulders. They also noted preferences of individual taxa for large particles because these were more stable and accumulated periphyton and coarse organic matter. Some of our findings are in agreement with these results. Thus, the scrapers *Rhitroperla rossi* and *Araucanioperla bullocki* were found only on cobbles and pebbles, where several shredders (*Chilenoperla puerilis*, *Klapopteryx kuscheli*, *Antarctoperla* sp.), which probably feed on trapped, fragmented detritus, were also common. On the other hand, several taxa did not show substratum preferences. The lack of specificity for a particular substratum noticed in the nominal shredders *Parasericostoma ovale* and *Brachysetodes major*, could indicate that these species have fairly general feeding habits. No studies have been undertaken on their feeding ecology, but VALVERDE & MISERENDINO (1997) suggested that at least *P. ovale* could complement its diet with epilithic algae.

The main taxa recorded on *Myriophyllum* in our study were the ubiquitous *Paratrichocladius* sp. (Chironomidae), a tipulid *Hexatoma*, and less commonly, the amphipod *Hyaella curvispina*. *Paratrichocladius* also co dominated with *H. curvispina* in a piedmont stream dominated by *Myriophyllum* (MISERENDINO & PIZZOLON 2000). In leaf packs, the shredders (*Brachysetodes major*) and collector-gatherers co-dominated, with scrapers, mainly represented by *Austrelnis* sp. (Elmidae), in third place. The numerical dominance of collector – gatherers, and biomass dominance of shredders in leaf packs is consistent with the findings of ALBARIÑO & BALSEIRO (2002) in other Patagonian streams.

Of the three species of *Meridialaris* (Leptophlebiidae) recorded in the present study, *M. chilocensis* seemed to be more habitat specific than *M. laminata* and *M. diguilina*. However, none of the species was recorded on sand. Indeed, practically no insects were recorded on sand where the more common species were Lumbriculidae, and less frequently, the gastropod *Chilina patagonica*. These findings are consistent with the results of an experimental study on the effects of sediment addition on stream fauna in Australia, which showed that high sediment levels caused a reduction in invertebrate density and diversity (DORG & MILLEDGE 1991). We suspect that an increase in fine sediment inputs could result in severe modifications to habitats and fauna in headwater streams in Patagonia, and there is evidence that invertebrate communities are disrupted by sediments derived from forestry and agricultural activities (PIZZOLON & MISERENDINO 2001).

Seasonal variation in discharge can play a major role in determining habitat and faunal persistence. Some mesohabitats (gravel) constitute discrete habitat units throughout the year, whereas others (macrophytes, silt, sand) may only be available in a particular season (ARMITAGE et al. 1995). At Nant y Fall the fauna on macrophytes and gravels differed more in spring than in summer as shown by the DCA. However, more species of macroinvertebrate were recorded on macrophytes in spring, suggesting that they may provide a refuge at the time of year when variable, high flows can be expected.

Except for macrophytes, sand and leaf packs, the CCA separated rivers more strongly than habitat types. Moreover, marked differences were found between macroinvertebrate assemblages in the dry and wet seasons. Current velocity, water temperature, depth and the amount of detritus were identified as important factors structuring macroinvertebrate communities. ERMAN & ERMAN (1984) also found that particle size, current velocity and detritus had major effects on the densities of species in Californian streams, and PARDO & ARMITAGE (1997) found that water velocity, flow dynamics and the nature of the substratum influenced the composition of benthic communities in streams of England.

As expected, large-bodied shredders dominated biomass in most habitats, confirming that energy resources were detrital based, as is common in low order forested streams (VANNOTE et al. 1980). Surprisingly, shredder density and biomass were higher among boulders and gravel than in leaf packs. In contrast, ANGRADI (1996) found that in some North American streams shredders were most abundant in leaf packs in pools, which were more retentive than riffles. We also found that organic matter was most abundant in pools. However, boulders had high contribution of shredders that were only recorded in hard substrata (e.g. *Senzilloides panguipulli*, *Chilenoperla puerilis*), whereas species of shredders recorded in leaf packs, were not limited to this habitat type.

Substratum type is one of the main environmental factors that affects distribution and abundance of lotic invertebrates (WRIGHT et al. 1983, MINSHALL 1984). However, as the water level rises and falls, stream habitat expands and contracts and resource availability changes (POWER et al. 1988). Then, shifts in detritus distribution can alter species distribution. Unstable substrata such as sand and leaves are easily affected by discharge, whereas larger particles such as boulders and cobbles are more stable. Thus, the substratum-taxon relationships observed in our study seem to be explained, in part, by substratum stability at the habitat scale. Our work indicates that riffles in low order Patagonian streams are persistent habitats, which have well-defined invertebrate assemblages that respond seasonally to changes in discharge, temperature and organic matter inputs. Changes in discharge, sedimentation, and inputs of organic matter derived from forestry activities can be expected to affect habitat quality and macroinvertebrate assemblages.

Additionally, headwater streams in Patagonia support a diverse fauna of exotic and endemic fishes that feed on invertebrates, including the introduced salmonids *Oncorhynchus mykiss*, *Salmo trutta* and *Salvelinus fontinalis* (ORTUBAY et al. 1997, PASCUAL et al. 2002). It is interesting that invertebrate diversity recorded at our study sites was lower than in similar stream environments in Australia where fish communities are not so diverse (MARCHANT et al. 1985, 1999). This suggests that predatory fish may be affecting the composition of invertebrate communities in low-medium order Patagonian streams as occurs in parts of New Zealand (MCINTOSH 2000). In some developed countries (e.g., England, United States) a sequence of linked management options (e.g., selective removal or addition of debris, retention of buffer strips) has been suggested to control sediments and organic matter transport within river systems draining catchments subject to commercial forestry, in order to enhance channel stability and physical habitat diversity (GURNELL et al. 1995). Although there is evidence that land development is affecting aquatic environments in Patagonia, mitigation practices have yet to be tested or implemented, adequately. The present study has provided much needed information on invertebrate assemblages and their environmental associations at the habitat scale and should help provide a baseline for conservation purposes and for the management of low order streams in Patagonia.

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