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Research Paper

Spatial and Temporal Pattern of Caddisfly Distribution at a Mesohabitat Scale in two Patagonian Mountain Streams Subjected to Pastoral Use

key words: Trichoptera, substrate, flow type, functional feeding groups

Abstract

Substrate, flow type, nutrients, aquatic vegetation, organic matter, and caddisfly community structure were studied at two low order streams (Glyn and Nant y Fall) subjected to pastoral use in the Patagonian mountains. At both sites, we examined the effect of habitat type (boulder-pebble with and without filamentous algae, cobble-pebble, gravel-sand, leaf-pack, the submerged macrophytes *Myriophyllum quitense* and *Isoetes savatieri*) and season (high and low water period) on caddisfly assemblages. Benthic particulate organic matter (BPOM) ranged between 4.6 and 472 g m⁻², all allochthonous detrital fractions were significantly higher at leaf-packs at Glyn, whereas *M. quitense* habitats supported more BPOM and macrophytes biomass at Nant y Fall. As expected, boulder-pebble sustained higher Trichoptera richness than *M. quitense* and gravel-sand, moreover all habitats showed higher density than *M. quitense* at Nant y Fall. According to our results at least nine caddisfly species exhibited some habitat preference with boulder-pebble and cobble-pebble the most selected habitat. These particular habitats sustained more than 68% of the total caddisfly species. Multidimensional scaling ordination highlighted differences in composition per habitat for both sites showing a clear distinction among depositional and erosional habitats. Substrate, flow type, detritus biomass were important predictors defining assemblages. Based upon our findings, those anthropogenic actions or stressors that change hydraulic as well substrate attributes in mountain streams such as stock trampling, dredging, clearing of riparian areas, will reduce caddisfly richness. These results are relevant for outline management and conservation biomonitoring and schemes in headwater Patagonian streams as well as other similar environments worldwide.

1. Introduction

Physical habitat heterogeneity is one of the main characteristic in stream ecosystems at a wide range of spatial scales, controlling macroinvertebrate abundance and diversity while it strongly influences the distribution of stream dwelling organisms (COOPER *et al.*, 1997; BOYERO, 2003; ALLAN and CASTILLO, 2007). In headwater streams, the physical habitats of benthic animals show contrasting changes at relatively small scales, thus generating consi-

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derable spatial heterogeneity for benthic organisms (SCHMERA *et al.*, 2007). For example the substratum provides habitat space for a variety of activities such as resting and movement, reproduction, rooting or fixing to, and for refuge from predators and flow. It also offers food directly (organic particles) or surfaces on which food aggregates (*e.g.*, algae, coarse and fine detrital particles) (GILLER and MALMQVIST, 1998; ALLAN and CASTILLO, 2007). As median particle size augments, physical complexity also increases. Mixed substrates would provide a greater range of surfaces to colonize and of microflow patterns (GILLER and MALMQVIST, 1998). It has been found that substrate stability is a good predictor of species assemblages and diversity (TOWNSEND *et al.*, 1997). On the other hand, organic substrate such as macrophytes, usually show a greater invertebrate abundance with large plant biomass, nevertheless species richness tends to be lower than the found in other substrates (COLLIER *et al.*, 1999). Alternatively, flow type, as a combination of velocity, flow direction and the influence of the substrate on the flow, influence the distribution of stream insect since they respond to current velocity rather than to absolute velocity (RAVEN *et al.*, 1998).

Water resources in Patagonia are being threatened by different anthropogenic practices; such as the impoundment of watercourses, channel realignment and dredging and the replacement of native forests and the conversion to pastures (MISERENDINO and BRAND, 2009; MISERENDINO *et al.*, 2011). The clearing of native forest to promote pastures, typically alters key aspects of stream habitat that influence invertebrate communities, including the type of food available, the physical shape of the stream, flow regime and water quality (WINTERBOURN, 1986; QUINN, 2000). An increase in fine sediment inputs sometimes could result in severe modifications to habitat and fauna in headwater streams in Patagonia, and there is evidence that invertebrate communities are disrupted by sediments derived from forestry and agricultural activities (VELÁSQUEZ and MISERENDINO, 2003a, 2003b; MISERENDINO and PIZZOLÓN, 2004; MISERENDINO *et al.*, 2011). Moreover, pasture streams are often enriched with nutrients that enhance plant growth, potentially affecting the ecology of streambed communities (QUINN, 2000).

Increasingly, a better understanding of the ecology and functioning of freshwater communities is needed, to face resource management and conservation purposes (HERING *et al.*, 2009). For river management schemes to be successful, ecological information that integrates physical and biological information is required. This is being achieved by using biological data to understand the role of physical features in determining the spatial distribution of organisms in streams (BUFFAGNI *et al.*, 2000; GUALDONI *et al.*, 2009).

Caddisflies constitute an important component of patagonian lotic environments, both in richness and abundance (ANGRISANO and SGANGA 2009). The group exhibits a high degree of endemism, which makes them extremely sensitive to environmental disturbances. Several studies address some relevant aspects of their ecology and distribution, as well as their response to habitat impoverishment (MISERENDINO, 1999, 2001; MISERENDINO and BRAND, 2007). Moreover, caddisfly species have been also used successfully in assessing physical and organic pollution (BRAND and MISERENDINO, 2008; BRAND *et al.*, 2010).

The aim of the present paper is 1) to analyze the affinity of caddisfly species to a specific habitat; 2) to examine the individual and joint effect of season and habitat type on the structural and functional properties of the caddisfly community and 3) to identify the main environmental variables, including energy resources, affecting caddisfly assemblages at the habitat scale on two mountain streams subjected to pastoral land use.

2. Study area

The study area belongs to the Andean-Humid and Sub-Andean Sub-Humid regions (PARUELO *et al.*, 1998) and is located in a transitional mountain and piedmont area in the Northwest of Chubut province, Argentina. From a phytogeographic perspective, the study area is located in the ecotone between the Subantarctic forest and the Patagonian steppe, and

exhibits a marked altitudinal gradient. Stream flow in the region is strongly linked to precipitation and snowmelt, which results in winter and spring spates. However, during summer, river flow is low and stable (CORONATO and DEL VALLE, 1988).

The catchment area of Nant y Fall is 161.8 km² and of Glyn is 21.7 km². The studied streams: Nant y Fall (3rd order) and Glyn (2nd order) are tributaries of the Futaleufú River and Corcovado River respectively. Nant y Fall dominant land use is pasture, whereas Glyn stream has a mixed management, with wood collection (*Nothofagus antarctica* and *N. pumilio*) and extensive livestock, mainly cows and sheep, which is sustained by the herbaceous stratum. The impact of these activities on both habitat in-stream, and riparian quality at these sites was documented in previous works by KUTSCHKER *et al.* (2009) and MISERENDINO and MASI (2010).

Dominant riparian vegetation at Glyn Stream is composed by native *Nothofagus antarctica* (30%), whereas the shrub coverage (40%) is represented by *Berberis buxifolia*, *Schinus patagonica*, *Maytenus chubutensis*, *Ribes cucullatum*, *Ovidia andina*, *Chusquea culeou*. Aquatic vegetation is composed mostly by *Veronica serpyllifolia*. Riparian vegetation at Nant y Fall stream is represented by some specimens of *Nothofagus antarctica*, *Schinus patagonica* and *Berberis buxifolia*. The dominant stratum is herbaceous (60 to 70%). Aquatic vegetation is diverse and composed by *Isoetes savatieri*, *Myriophyllum quitense*, *Limosella australis*, *Ranunculus flagelliformis* and *Callitriche lechleri*; the subemergent *Lilaeopsis macloviana* and *Mimulus glabratus*; and the emergent macrophytes *Veronica anagallis-aquatica*, *Eleocharis albibracteata*, *Juncus burkartii*, *J. diemii* and *J. microcephalus*.

3. Materials and Methods

3.1. Sampling Design and Reach Characterization

Nant y Fall and Glyn rivers were visited twice, during high (October 2007) and low water periods (March 2008); the selected sites were at comparable elevation (690 and 615 m.a.s.l. respectively). At each site, percentages of boulder (> 25 cm), cobble (6.4–25 cm), pebble (1.6–6.4 cm), gravel (2–16 mm), and sand (0.25–2 mm) in the reach were estimated using a 1 m² grid (WARD, 1992). Current speed was measured in mid channel (average of three trials) by timing a float as it moved over a distance of 10 m (GORDON *et al.*, 2004). Average depth was estimated from five measurements with a calibrated stick along a transverse profile across the channel. Wet and dry widths (from bank to bank) of the channel were also determined. Discharge (m³ s⁻¹) was obtained by combining depth, wet width and current velocity as in GORDON *et al.* (2004).

On each sampling occasion water temperature, pH, specific conductivity ($\mu\text{S}_{20} \text{cm}^{-1}$), dissolved oxygen (mg O₂ l⁻¹), oxygen saturation percentage, and total dissolved solids (TDS) (mg l⁻¹) were measured with a multi-parameter probe (Hach SensION 156). For nutrient analyses water samples were collected below the water surface, kept at 4 °C and transported to the laboratory for analysis. Total nitrogen (TN) and total phosphorus (TP) were determined on unfiltered samples digested with persulphate, whereas nitrate (NO₃), ammonia (NH₄), and soluble reactive phosphate (SRP) were analyzed using standard methods (APHA 1999).

3.2. Habitat Selection

Flow type, dominant substrate, depth and vegetation were used to define each habitat type. Flow types were assessed according to URBANIC *et al.* (2005) and classified as no perceptible flow (1), smooth flow (2), lateral moving water (3), unbroken standing waves (4), and chute flow (5). Dominant particles of substrate were assessed visually and depth was measured at each habitat with a calibrated stick. The macrophytes, *Myriophyllum quitense* (Haloragaceae) and *Isoetes savatieri* (Isotaceae) were consistently represented in both spatial and season and then selected as possible habitats in the design.

Table 1. Geographic coordinates and elevation of both sampling sites and main characteristics of habitat types selected in Nant y Fall and Glyn stream, Patagonia (Argentina). Flow type references: 1: no perceptible flow; 2: smooth flow; 3: lateral moving water; 4: unbroken standing waves; and 5: chute flow.

	Nant y Fall					Glyn				
Geographic coordinates	43°13'24" S – 71°25'17" W					43°27'34"S – 71°33'25" W				
Elevation (m.a.s.l.)	690					615				
Microhabitat	M	CP	BP	IS	GS	LP	BF	CP	GS	BP
Dominant substrate	Sand Silt	Cobble Pebble	Boulder cobble	Cobble pebble sand	Gravel sand	Sand	Boulder cobble	Cobble pebble	Pebble sand	Boulder cobble
Flow type	1	4	5	4	3	1	5	3	2	4
Water depth (cm)	44	23	17.3	26.5	36.1	31.3	11.16	15.5	36	23
Dominant vegetation	<i>Myriophyllum quitense</i>		<i>Isoetes savatieri</i>			Fila-mentous algae				

A total of seven different habitat types were identified. In depositional areas (pools) three habitat types were sampled: gravel-sand (GS), leaf-pack (LP) and macrophytes (*M. quitense*) (M). In riffle areas two different habitats were sampled: boulder-pebble (BP) and boulder-pebble with filamentous algae (BF). In run areas cobble-pebble (CP) and cobble-pebble with the submerged *I. savatieri* (IS) were examined. Habitat GS, BP and CP were common at both, Glyn and Nant y Fall rivers, whereas LP was present at Glyn and M and IS at Nant y Fall (Table 1).

3.3. Caddisfly Sampling

Three Surber samples (0.09 m², 250 µm mesh size) were taken at each habitat in each stream, during the dry and wet seasons, summarizing 60 samples. Samples were fixed with formaldehyde in the field. Individuals and detritus from each sample were sorted in the laboratory.

Sorting involved elutriation and the collection of materials on a series of sieves (mesh width 250 µm and 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), seeds, and others (fragments of leaves, grass, roots, buds, etc.) (VOELZ and WARD, 1990). All fractions were dried (110 °C for 4 h) and weighted on an electronic balance to ± 0.5 mg.

Larvae were sorted manually under 5 × magnification, counted and preserved in 70% alcohol. Caddisfly larvae were identified to the lowest possible taxonomic level using available keys (ANGRISANO, 1997, 1998; SGANGA and ANGRISANO, 2005; ANGRISANO and SGANGA, 2009). Density was calculated from counting all the individuals in a sample. Functional feeding groups were assigned by gut analyses and using available references (MERRITT *et al.*, 2008; BRAND and MISERENDINO, 2011a, 2011b).

3.4. Statistical Analyses

Fixed-effects 2-factor ANOVA models were used to assess significant differences in species richness, total density, Shannon diversity, autochthonous and allochthonous organic matter between habitats (5) and dates (2). The interaction between habitat and season was also assessed. Comparisons among habitats

were performed later with Tukey's (HSD) test ($P < 0.05$). Variables were transformed by $\log(x + 1)$ to improve normality prior running ANOVA, and homogeneity of variances was tested using Levene's test.

To examine the preference of species to a particular habitat, differences on density per habitat were assessed using non parametric Kruskal-Wallis test (SOKAL and ROHLF, 1995).

To investigate the relation between habitat, environmental variables and functional feeding groups at each stream, a multidimensional scaling (MDS) analysis was performed. This non linear ordination procedure is an alternative to the factorial method and the objective is to display significant distances among investigated objects (LUDWIG and REYNOLDS, 1988). Pearson correlation matrixes based on quantitative macroinvertebrate data and habitat types (high and low period) were carried out for each stream: Nant y Fall (16 sp \times 30 samples) and Glyn (16 sp \times 30 samples). These matrixes were employed to produce the MDS ordinations. Dimension scores from MDS can be related to environmental variables to reveal ecological patterns (HAWKINS *et al.*, 1997; MALONEY and FEMINELLA, 2006). The dimensions (MDS1 and MDS2) were extracted, and the influence of the environmental variables was assessed with single regression analysis (TER BRAAK, 1992). All the environmental variables presented in table 2 and 3 were used in the analysis. Same procedure was employed to relate community attributes with MDS dimensions to determine which group of taxa best accounted for separation of habitats in ordination space.

4. Results

Water temperature, both maximum and minimum, were higher at Nant y Fall than at Glyn stream (Table 2). Conductivity values for Nant y Fall were 80.4 and 105.1 $\mu\text{S cm}^{-1}$, during high and low water periods respectively, whereas at Glyn, ranged from 30.1 to 56.6 $\mu\text{S cm}^{-1}$. Dissolved oxygen varied from 9.95 to 13.88 mg l^{-1} at Nant y Fall, and from 7.88 to 14.97 mg l^{-1} at Glyn stream. Oxygen saturation percentage and nutrient values were similar at both sites (Table 2). Although dissolved oxygen percentage diminished in low water period at both sites, at Glyn was 42% lower than Nant y Fall.

As expected, autochthonous organic matter was the best represented material at Nant y Fall stream (Table 3), being macrophytes biomass significantly higher at habitats M and IS than at CP, BP and GS (ANOVA, $P < 0.005$, Table 4). The item filamentous algae were the

Table 2. Environmental variables at Nant y Fall and Glyn Streams (Patagonia, Argentina), for high and low water periods, October 2007 and March 2008, respectively.

Variable	Nant y Fall		Glyn	
	High	Low	High	Low
Wetted width (m)	17.2	16	3.88	3.5
Depth (m)	0.37	0.21	0.29	0.17
Current speed riffle (m sec^{-1})	0.88	0.33	1.03	0.64
Current speed pool (m sec^{-1})	0.55	0.22	0.69	0.3
Water temperature ($^{\circ}\text{C}$)	8.3	18.7	5	12.4
pH	8.17	8.28	7.07	7.21
Dissolved oxygen (mg l^{-1})	13.88	9.95	14.97	7.88
Saturation %	121.4	114.4	118.4	72.3
Conductivity ($\mu\text{S cm}^{-1}$)	80.4	105.1	30.1	56.6
TDS (mg l^{-1})	57.71	57.5	22.4	35.4
Ammonia (NH_4) ($\mu\text{g l}^{-1}$)	9	6	4.5	4.5
Soluble reactive phosphorus ($\mu\text{g l}^{-1}$)	2	1.5	4	4
Nitrate (NO_3) ($\mu\text{g l}^{-1}$)	2.5	2.5	11	4
Total phosphorus ($\mu\text{g l}^{-1}$)	23	50	28	80
Total nitrogen ($\mu\text{g l}^{-1}$)	205	171	153	175
TSS ($\mu\text{g l}^{-1}$)	8.8	1.7	2.8	0.7

Table 3. Organic matter biomass (dry mass g m^{-2}). Values of high (left) and low (right) water periods (October 2007 and March 2008, respectively), for each habitat, at Nant y Fall and Glyn streams Patagonia, Argentina.

	Nant y Fall						Glyn					
	M	CP	BP	IS	GS	LP	BF	CP	GS	BP		
Filamentous algae	0	0–0.1	0–0.15	0	0	0	0–10.5	0–0.06	0–2.6	0.04–0		
Mucilaginous algae	0.10–0.7	0.05–0.2	0.1–0.03	0.3–0.03	0–0.44	0	0	0	0	0		
Bryophytes	7–3.7	1.1–1.3	15.1–0.8	3–0.5	1.3–2.1	0.9–4.1	0.2–4.9	0.2–0.2	0.6–0.8	1.1–1.1		
Macrophytes	46.3–82.6	0.5–0.4	3.4–9.5	78.1–67.8	5.4–12.4	0	1.6–0.8	0.7–0.2	0.2–6.3	0–0.1		
FPOM	31.75–24.4	2.6–3	7.8–3.2	4.9–5.9	5.3–4.6	23–15.7	10.2–1.7	5.5–2.7	5.6–9.7	5.1–2.8		
Others	24.23–10	2.1–1.8	6.8–4.4	8.1–6.1	5.7–3.8	79.8–67	2.9–2.5	3–2.4	2.7–10.2	3.1–1.6		
Leaves	2.95–1.4	0.2–0.06	0.2–0.8	0.2–0	0.5–0.9	135.2–56.4	10.3–9.5	11.8–1.8	7.6–3.5	14.7–1.5		
Wood	14.4–5.6	0.2–0.2	0.7–1.8	1.4–0.4	39.6–2.8	120.6–320	9.1–14.3	6.6–5.7	7.3–9.2	4.6–15.3		
Seeds	3.8–0.1	0.3–0.1	0.5–0.4	0.3–0.1	0.4–0.1	13.1–10.3	1.7–1.9	1.7–1	1.4–0.3	1.1–0.8		
CPOM	45.46–17.2	2.9–1.6	8.23–7.35	10.06–6.5	46.3–7.73	348.8–457	24.02–28.3	23.11–11	19–23.32	23.52–19.2		
BPOM	77.21–41.6	5.5–4.6	16.06–10.6	15–12.43	51.6–12.3	372–472.6	34.28–30	28.67–13.7	24.7–33	28.6–22.1		

Table 4. Results of factorial ANOVAs examining the effects of season and habitat on species richness, total density, Shannon diversity index (H'), autochthonous and allochthonous detrital fractions in 5 habitats, sampled during high (H) and low (L) water periods at the studied streams, Patagonia, Argentina. M: Macrophytes; CP: cobble-pebble; BP: boulder-pebble; IS: *Isoetes*; GS: gravel-sand; LP: leaf-pack; BF: boulder with filamentous algae. * $P < 0.05$ and ** $P < 0.005$.

	Nant y Fall				Glyn			
	Season $F_{(1,20)}$	Habitat $F_{(4,20)}$	Season x Habitat $F_{(4,20)}$	Observed relationship	Season $F_{(1,20)}$	Habitat $F_{(4,20)}$	Season x Habitat $F_{(4,20)}$	Observed relationship
Species richness	37.53**	10.84**	2.37	H > L BP > M, GS	0.01	1.69	2.21	
Total density	15.11**	26.41**	7.04*	H > L CP, BP, IS, GS > M BP > IS	0.01	1.20	1.42	
H'	2.55	6.63**	10.03**	GS > M	0.27	0.83	2.52	L > H
Fl. algae	1.93	0.83	0.83	BP > IS	34.53**	16.53**	16.92**	BF > LP, CP, BP
Bryophytes	2.58	1.68	0.98	M, IS > CP, BP, GS	4.24	1.76	1.47	
Macrophytes	5.86	61.04**	1.47	GS	0.01	1.43	0.91	
FPOM	0.44	18.98**	0.54	M > CP, BP, IS, GS	11.42	14.06	3.79	
Others	4.38**	11.69**	0.38	H > L M > CP, BP, GS IS > CP	0.01	26.80**	0.88	LP > BF, CP, GS, BP
Leaves	0.01	6.18**	0.78	M > CP, BP, IS	17.56**	21.86**	1.36	H > L LP > BF, CP, GS, BP
Wood	3.69	5.20**	1.42	M > CP GS > CP	1.39	10.78**	0.63	LP > BF, CP, GS, BP
Seeds	6.40*	1.56	1.70	H > L	1.21	20.28**	0.61	LP > BF, CP, GS, BP
CPOM	5.97*	8.98**	0.83	M > CP, BP GS > CP	0.36	21.72**	0.35	LP > BF, CP, GS, BP
BPOM	3.24	10.95**	0.42	M > CP, BP, IS GS > CP	0.61	23.05**	0.28	LP > BF, CP, GS, BP

Table 5. Functional feeding groups (FFG), relative abundance of 22 Caddisfly taxa (%), total richness (cumulative values), density (ind. m⁻²) and Shannon diversity (H'), in different habitat types of two low order streams of Patagonia (Argentina). Scr: Scrapers; P: Predators; Sh: Shredders and CF: Collector-filterers. M: *Myriophyllum quitense*; CP: cobble-pebble; BP: boulder-pebble; IS: *Isoetes savatieri*; GS: gravel-sand; LP: leaf-pack; BF: boulder-pebble with filamentous algae.

	FFG	Nant y Fall					Glyn				
		M	CP	BP	IS	GS	LP	BF	CP	GS	BP
Glossosomatidae											
Hydrobiosidae											
<i>Cailloma pumida</i> ROSS, 1956	P	0	0	0	0	0	0	4.5	16.7	0	24.2
<i>Metachorema griseum</i>	P	0	0.3	0.6	0.1	0.1	0	0	0	0	0
<i>Neatopsyche brevispina</i> SCHMID, 1957	P	0	0.6	0.6	0.3	0.4	0	40.9	10	0	4.5
<i>Neatopsyche unispina</i> FLINT, 1967	P	0.6	0.3	0.3	0.9	0.5	0	18.2	5	27.3	4.5
<i>Neopsilochorema tricarinatum</i> SCHMID, 1955	P	0	1.6	0.6	0.1	0.2	0	0	10		9.1
<i>Rheochorema lobuliferum</i> FLINT, 1967	P	0	0	0.1	0	0	0	4.5	11.7	9.1	13.6
<i>Rheochorema robustum</i> SCHMID, 1955	P	0	0	0	0	0	0	4.5	0	0	0
<i>Rheochorema tenuispinum</i> SCHMID, 1955	P	0	0	0	0	0	4.7	9.1	5	0	0
Hydropsychidae											
<i>Smicridea annulicornis</i> (BLANCHARD, 1851)	CF	0	2.8	10.1	1.4	0.1	0	0	6.7	0	13.6
<i>Smicridea frequens</i> (NAVÁS, 1930)	CF	0.6	9.5	32.1	11.9	0.6	0	0	0	0	0
Hydroptilidae											
<i>Oxyethira bidentata</i> MOSELY, 1934	Scr	9.1	0.2	0.1	0.6	0	9.5	0	3.3	18.2	0
Leptoceridae											
<i>Brachysetodes quadrifidus</i> SCHMID, 1955	Sh	1.7	0.5	0.2	1.5	0.3	38.1	13.6	5	45.4	0
<i>Hudsonema flaminii</i> (NAVÁS, 1936)	Sh	23.8	0	0	0	0.8	4.7	0	0	0	0
<i>Tripletides</i> sp.	Sh	0	0	0	0	0.1	19.1	0	0	0	0
Limnephilidae											
<i>Monocosmoecus</i> sp.	Sh	28.4	0.1	0.1	1	0.8	4.8	0	0	0	0
<i>Verger</i> sp. 1	Sh	2.8	0.6	0.1	0.2	0.1	0	0	0	0	0
<i>Verger</i> sp. 2	Sh	0	0	0	0.1	0	0	0	0	0	0
Philorheithridae											
<i>Psilopsyche molinae</i> NAVÁS, 1926	P	0	0	0	0	0	0	0	3.3	0	1.5
Polycentropodidae											
<i>Polycentropus</i> sp.	P	0	0	0	0	0	0	4.5	23.3	0	27.3
Sericostomatidae											
<i>Myotrichia murina</i> SCHMID, 1955	Sh	0	0	0	0	0	19.1	0	0	0	1.52
<i>Parasericostoma ovale</i> (SCHMID, 1955)	Sh	32.9	82.7	55	81.8	95.7	0	0	0	0	0
Total richness		8	12	13	12	12	7	8	11	4	9
Density		326	2290	7135	2272	1526	39	41	55	20	122
Shannon Diversity		1.51	0.73	1.07	0.72	0.27	1.66	1.73	2.21	1.24	1.87

least abundant, being present only at CP and BP habitats (0.1 and 0.15 g m^{-2} , respectively) (Table 3). Although bryophytes exhibited the highest biomass values at M and BP no significant relationships were observed. Habitat M showed the highest BPOM biomass (77.21 g m^{-2}) during the high water period. This fraction was between 1.9 and 12 times higher in this habitat than the rest. ANOVA results showed that BPOM was significantly higher at M than CP, BP and IS, and that at GS was higher than CP. On the other hand, the item leaves was consistently higher at M than CP, BP and IS ($F = 6.18$ $P < 0.005$) (Table 4). Concerning FPOM biomass, values ranged from 2.6 (CP) to 31.75 g m^{-2} (M) and habitat M supported significantly more FPOM than the rest of the habitats ($F = 18.9$, $P < 0.005$). At this stream the items seeds and others were significantly higher during the high water period (Table 4).

At Glyn stream wood and leaves were the best represented detrital item at LP habitats (Table 3), reaching values of 320 and 135.2 g m^{-2} respectively. Factorial ANOVA indicated that LP had higher contribution of all fraction of allochthonous coarse matter including others, leaves, wood, seeds, CPOM and BPOM than the rest of the habitats (ANOVA, $P < 0.005$). Regarding seasonal differences only leaves and filamentous algae showed a consistent pattern, being leaves biomass significantly greater during the high water period. The opposite trend was observed for filamentous algae (ANOVA, $P < 0.005$), therefore dominating in summer samples.

Caddisfly community was composed by 22 taxa grouped in nine families being Hydrobiidae the best represented (8 species). *Parasericostoma ovale* showed the highest contribution in relative abundance at all Nant y Fall habitats (Table 5). At Glyn stream *Brachysetodes quadrifidus* dominated at LP and GS, *Neoatopsyche brevispina* at BF, and *Polycentropus* sp. at CP, on the other hand *Cailloma pumida* and *Polycentropus* sp. codominated at BP. Total richness ranged from 4 (Glyn, at GS) to 13 taxa (Nant y Fall, at BP). Lowest density values were recorded at Glyn stream (20 to 122 ind. m^{-2} , at GS and BP respectively), Nant y Fall values were at least three times higher than maximum values reported at Glyn (326 to 7135 ind. m^{-2} , M and BP respectively). Shannon diversity index ranged from 0.27 to 1.87 bits (GS, Nant y Fall and BP, Glyn respectively).

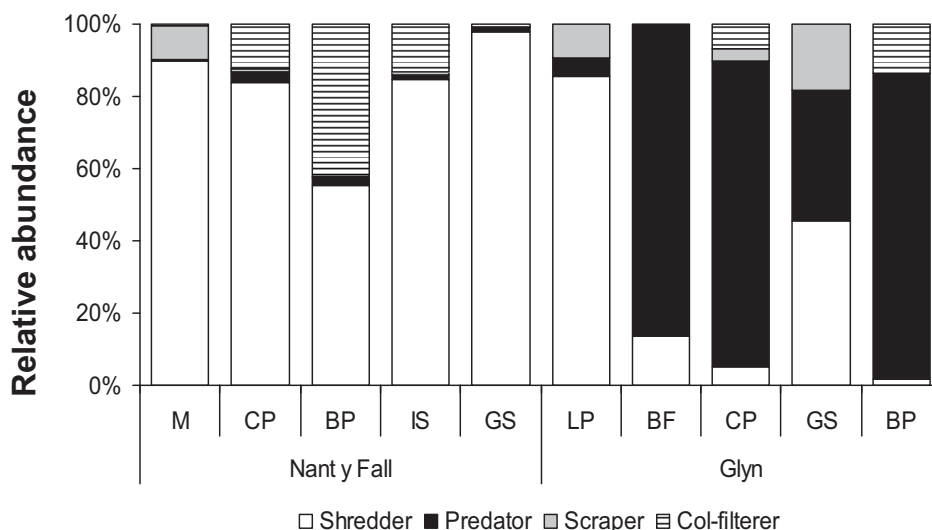


Figure 1. Relative abundance of Trichoptera functional feeding groups, for each habitat type, at two low order streams of Patagonia (Argentina). Data from October 2007 and March 2008, surveys.

Differences among habitats were significant for species richness with BP supporting more species than M and GS ($F = 10.84$, $P < 0.005$) at Nant y Fall stream. Instead total density was significantly lower at M than the rest ($F = 26.41$, $P < 0.005$), and diversity was consistently higher at BP than at IS ($F = 6.63$, $P < 0.005$). Caddisfly richness and density were significantly higher during the high water period (Table 4). We did not detect significant differences in species richness, density and diversity among habitats or seasons at Glyn stream.

Shredders were the best represented FFG at all Nant y Fall habitats, while at Glyn stream this group contributed with almost 50% of the total community at LP and GS. The habitats BF, CP and BP (Glyn) were dominated by predators, mainly species belonging to Hydrobiosidae family (Fig. 1). Collector-filterers contributed with 42.3% of the caddisfly assemblage at BP (Nant y Fall) whereas scrapers reached 18.2% at GS (Glyn stream) (Fig. 1).

Mean abundance of some taxa displayed considerable variation between habitats, however at least 9 taxa showed affinity for some particular type of habitat (Fig. 2). According to Kruskal-Wallis analysis *P. ovale*, *N. unispina*, *M. longicornuta*, *M. griseum*, *S. annulicornis*,

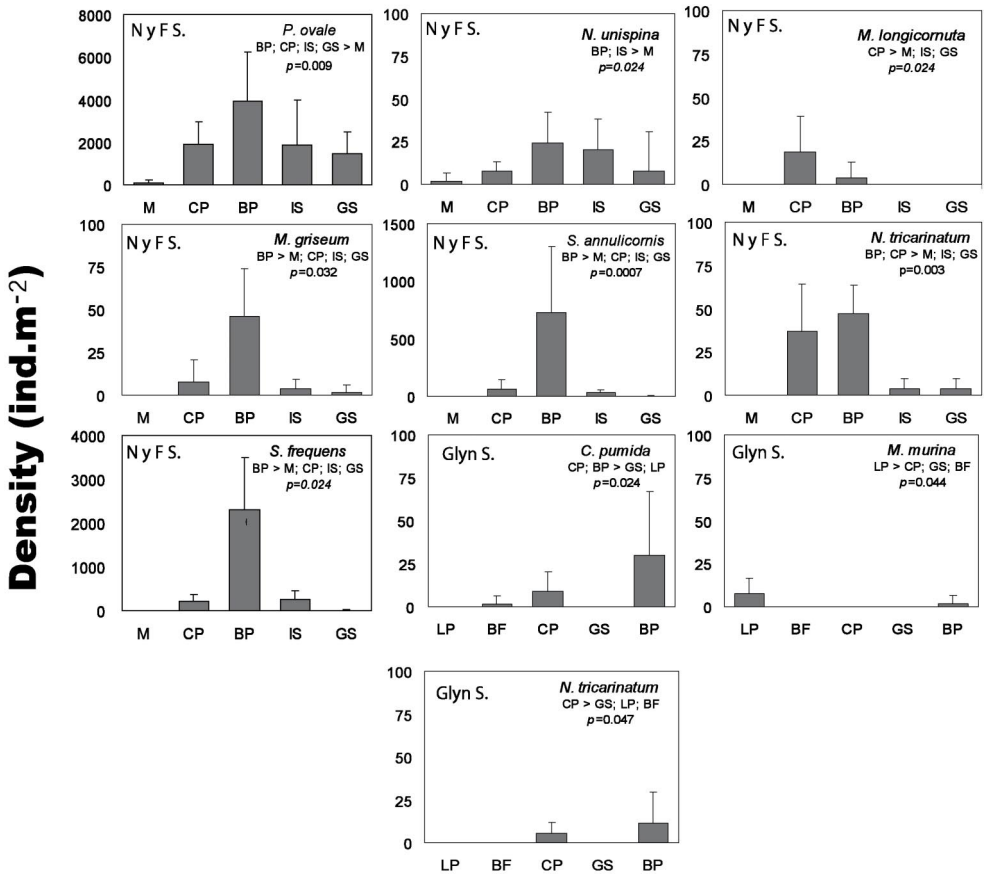


Figure 2. Mean abundance (ind. m⁻²) for each habitat for the nine taxa that showed preference for some habitat type (October 2007 and March 2008) at two low order streams of Patagonia (Argentina). Relationships and p values (Kruskal-Wallis analysis) are given for each taxon. Bars represent ± 1 SD ($N = 6$).

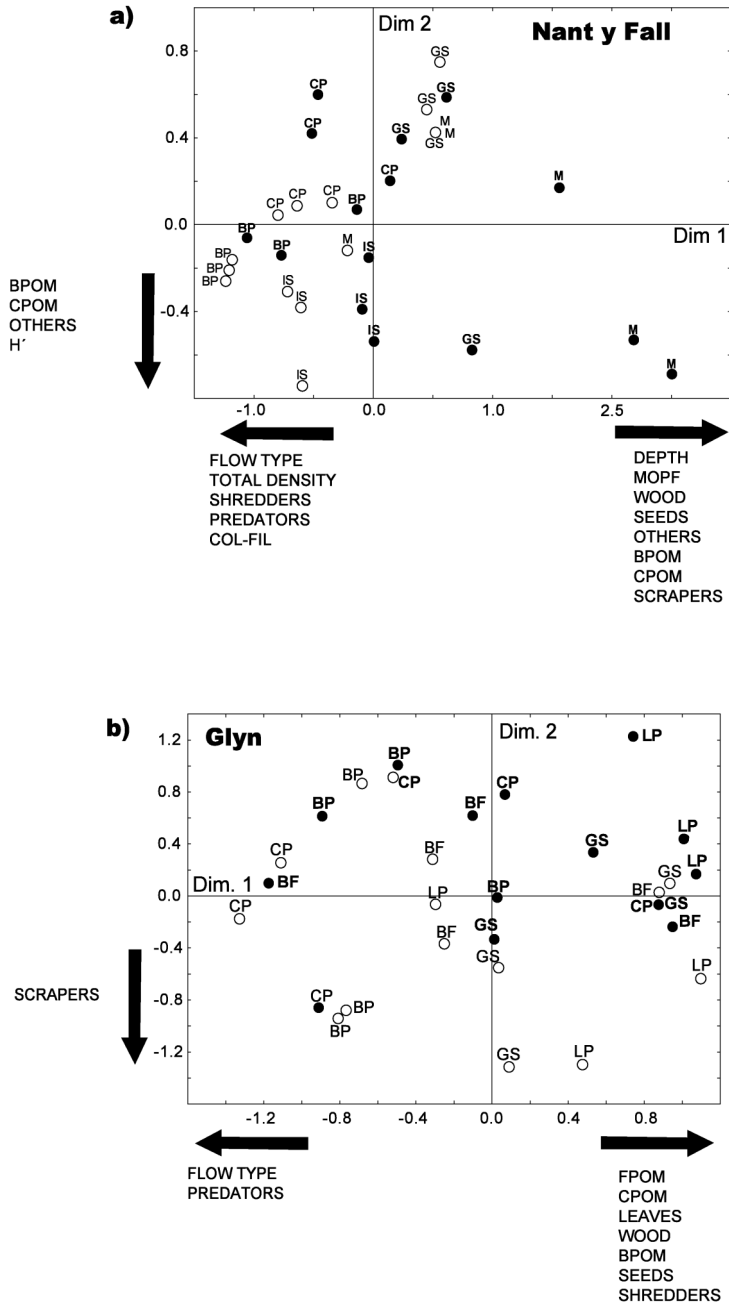


Figure 3. MDS ordination for a) Nant y Fall and b) Glyn streams. All variables correlated (Spearman correlation coefficient, $P < 0.05$) with dimension one and two are marked in margins of each graph, at two low order streams of Patagonia (Argentina) (October 2007 and March 2008). Filled circles: high water period, open circles: low water period. M: *Myriophyllum quitense*; CP: cobble-pebble; BP: boulder-pebble; IS: *Isoetes savatieri*; GS: gravel-sand; LP: leaf-pack; BF: boulder-pebble with filamentous algae.

S. frequens and *N. tricarinatum* at Nant y Fall stream, and *N. tricarinatum*, *C. pumida* and *M. murina* at Glyn stream showed significant differences in density distribution among habitats ($P < 0.05$) (Fig. 2). Most of these species preferred coarse inorganic substrate, such as BP and CP. *M. griseum*, *S. annulicornis* and *S. frequens* seemed to prefer BP to the rest of the habitats assessed (Fig. 2). *C. pumida* (Glyn) and *N. tricarinatum* (Nant y Fall) showed affinity for both CP and BP habitats. *N. tricarinatum* also showed preference for CP (Glyn). Similarly *M. longicornuta* had significantly higher density at CP than M, IS and GS (Kruskal-Wallis, $P = 0.024$). On the other hand, *N. unispina* exhibited more affinity for BP and IS than for M. *P. ovale* showed a significantly lower abundance at M than all other habitats, while *M. murina*, preferred LP over coarse substrates (Fig. 2).

MDS ordination highlighted differences in caddisfly composition among habitat types for both sites. Several environmental variables were clearly associated with MDS dimensions 1 and 2. A clear distinction between depositional (M and GS) and erosional (BP, CP and IS) habitats were detected along the dimension 1 at Nant y Fall stream (Fig. 3a). Variables that clearly defined the gradient of environmental conditions were depth and flow type (Fig. 3a, Table 6). M habitat, with slow flow and a greater depth was clearly associated with positive values of dimension 1 (Table 6). On the contrary, the habitats BP, CP and IS were placed towards the negative side of MDS1. Other environmental variables with explanatory power and associated with MDS1 were MOPF, leaves, BPOM and CPOM (Fig. 3a). Habitats IS and BP were grouped to the negative side of MDS2 whereas mostly GS and CP to the positive side of this dimension. Variables that significantly augmented towards the negative side of MDS2 were BPOM, CPOM and others. FFG that grouped on the negative side of MDS1

Table 6. Environmental and biological variables regressed (r^2) with dimensions 1 and 2 of MDS based on Trichoptera density data at a mesohabitat scale at Nant y Fall and Glyn streams Patagonia Argentina. Significance: * $P < 0.05$, ** $P < 0.005$. FFG: Functional Feeding Groups.

Variable	Nant y Fall		Glyn	
	Dimension 1	Dimension 2	Dimension 1	Dimension 2
<i>Environmental variables</i>				
Depth	0.77**	ns	ns	ns
Flow type	-0.64**	ns	-0.17*	ns
FPOM	0.35*	ns	0.26**	ns
Others	0.46*	-0.17*	ns	ns
Macrophytes	ns	ns	ns	ns
Leaves	0.38*	ns	0.19*	ns
Wood	ns	ns	0.10*	ns
Seeds	0.25*	ns	0.17*	ns
CPOM	0.29*	-0.13*	0.17*	ns
BPOM	0.40**	0.12*	0.17*	ns
<i>Community attributes</i>				
Richness	ns	ns	ns	ns
Total density	-0.12*	ns	ns	ns
Shannon diversity	ns	-0.48**	ns	ns
<i>FFG</i>				
Shredders	-0.10*	ns	0.47**	ns
Predators	-0.30**	ns	-0.42**	ns
Scrapers	0.19*	ns	ns	-0.24*
Collector-filterers	-0.33**	ns	ns	ns

were shredders, predators and collector-filterers, as well as total caddisfly density (Fig. 3a, Table 6).

Unsurprisingly, Glyn stream had a less clear distinction between habitats, thus there were no clear association of caddisflies species for particular habitats. However, MDS1 showed a gradient between high retentive habitats (LP, GS, BF mainly), with higher biomass of most organic fractions on the positive values whereas habitats having higher current speed (BP and CP) were placed on the negative values of this dimension. Predators were grouped on the negative side of MDS1, while shredders appeared on the positive side of that dimension. On the other hand scrapers were associated to the negative side of MDS2 (Fig. 3b, Table 6).

5. Discussion

Observed differences in caddisfly community attributes were significant at Nant y Fall habitats whereas this did not happen at Glyn stream. Accordingly, in terms of species richness and density, coarse substrates (BP) at Nant y Fall supported more species and organisms, than depositional areas with or without macrophytes (M and GS). This pattern is consistent with the findings of VELÁSQUEZ and MISERENDINO (2003b) at four Patagonian streams where run-riffles sustained higher densities and biomass of invertebrates than sandy pools. At our work, most caddisfly species recorded showed preference for inorganic coarse substrates, such as boulder-pebble and cobble-pebble whereas sand and gravel were the least preferred habitats. Likewise, URBANIC *et al.* (2005) observed that most caddisfly species selected coarse substrates in shallow water with chute flow, whereas fewest were found on fine substrate in deep water at European rivers.

According to the literature, macrophytes with an intricate morphology harbor a higher invertebrate abundance than more simply structured plants habitats do (HAUSER *et al.*, 2006; WARFE and BARMUTA, 2006). However, in our work total richness and total density were significantly higher at the less complex lycopsid *Isoetes savatieri* than at *Myriophyllum quitense* with a higher intricate morphology. Contrarily to our results, HANSEN *et al.* (2010) found that total macroinvertebrate abundance on the structurally complex *Myriophyllum spicatum* was significantly higher than on to more simply structured *Potamogeton pectinatus* and *Chara baltica*. In our study the macrophyte *I. savatieri* showed a dense coverage in runs areas whereas *M. quitense* at pools. Likely, IS habitat offers more suitable refuge from predators such as fish but also showed more favorable environmental conditions of flow and food.

In this study, the shredder *Parasericostoma ovale* was the most important species in terms of density and was represented in all habitats even those with the aquatic perennial *I. savatieri*, which sustained more individuals than *M. quitense*. According to previous works *P. ovale* lacks preference for a particular substratum and shows flexible feeding habits, seeming to alternate their diet with epilithic algae and FPOM (VALVERDE and MISERENDINO, 1997; VELÁSQUEZ and MISERENDINO, 2003b). As expected, the shredder *Myotrichia murina* was strongly associated to leaf-packs habitat and secondarily to boulder-pebble. Allochthonous detrital fractions (leaves, wood, seeds and others) appear as predictors of abundance of this species as evidenced in the NMS. The scraper *Mastigoptila longicornuta* preferred CP habitats. SCHMERA and EROS (2004) found that the percentage of scraper caddisflies increased at riffle habitats in Hungarian streams, accordingly URBANIC *et al.* (2005) found that the scraper *Goera pilosa* (Goeridae) was strongly associated with cobbles in European rivers. It seems that cobbles with rough texture in run areas appear to be the optimum substrates to periphyton growth (BOYERO, 2003). The shredder *Hudsonema flaminii* was reported in higher density at *M. quitense* habitats, although this pattern was not statistically consistent. Due to the sampling method applied in this study we probable missed some riparian environment as marginal habitats and submerged grasses that may sustain several species and feeding groups. Late instars of *H. flaminii* have been recorded in connected pools on marginal areas

at other patagonian streams (Pers. obs.) and this particular habitat should be considered and included in future studies.

Flow type classification, based on velocity, flow direction and substrate roughness, is referred to as the most important hydraulic component on macroinvertebrate assemblages. Stream insect and particularly filter feeders; respond to current velocity rather than to absolute velocity (RAVEN *et al.*, 1998). In our study, flow type was an important variable determining caddisfly FFG arrangement along the habitats selected as shown by the MDS ordination. Both predators and collector-filterers peaked in sites with high flow type values at both streams. As we observed, there was a strong affinity of the Hydropsychidae species *S. annulicornis* and *S. frequens* to boulder-pebble substrates. SMITH-CUFFNEY and WALLACE (1987) also suggested that rockface tend to be more productive in terms of filter-feeder species than deep riffles or sandy substrates, probably this habitat improves the effectiveness of filterers nets. Moreover, STATZNER (1981) reported that *Hydropsyche* spp. showed high abundances when hydraulic stress also increased. Shallow run-riffle habitats with coarse substrate and low amounts of CPOM seems to be preferred by filter-feeders as documented in recent investigations (BUFFAGNI *et al.*, 2000; URBANIC *et al.*, 2005; CHAKONA *et al.*, 2008).

SCHMERA and ERÖS (2004) also found that, while scrapers and collectors tend to inhabit riffles, predators occupy pools; their findings were also in agreement with the statements of MERRITT and CUMMINS (1996) and WEIGEL *et al.* (2003). Nevertheless, our study showed that most predators (*Metachorema griseum*, *Neopsilochorema tricarinatum* and *Cailloma pumida*) preferred boulder-pebble and cobble-pebble substratum, furthermore, MDS ordination showed a strong association between this group and high flow type values.

Moreover it is known that at headwater streams, habitats dominated by fine sediment are unstable facing hydraulic stress and few species are adapted to inhabit them (WARD, 1992). This was supported by our observations, given that gravel-sand habitats were less diverse and sustained low caddisfly density. CHAKONA *et al.* (2008) observed that habitat simplification through siltation may significantly decline diversity of aquatic insects in African rivers, possibly through reduction of available refugia and diminution of habitat stability. Sedimentation process also has detrimental effects on organisms as a result of the scouring during high discharge events (QUINN, 2000). Filter-feeder caddisfly species (*e.g.*, Hydropsychidae) are strongly affected by siltation since their nets become inoperable under conditions of increased sediment deposition and transport (GURTZ and WALLACE, 1984; SMITH-CUFFNEY and WALLACE, 1987).

Conversion of native forest and shrub lands to pastures is acquiring increasing importance in Patagonia. The clearing of riparian areas, alters the functioning of river ecosystems, and aquatic biota may result affected directly or indirectly, by increasing sediment inputs and altering flow characteristics (MISERENDINO *et al.*, 2011) or by disruption of matter and energy fluxes (MCCORD *et al.*, 2007). Moreover, pastoral development often produces alteration of stream habitat for example through livestock trampling which results in important sedimentation symptoms (WINTERBOURN, 1986; QUINN, 2000; BUSS *et al.*, 2004).

An accurate identification of distinct habitats in the aquatic and riparian environment has been advocated by many authors as a valuable tool for use in monitoring programmes, as well as in ecologically sensitive river management schemes (BUFFAGNI *et al.*, 2000). As a species rich and ecologically diverse insect order, caddisflies are well-suited to reflect the intensity of different stressors on aquatic ecosystems (HERING *et al.*, 2009). Therefore, we consider that a better understanding of the habitat preferences of caddisfly species is essential for conservational schemes definition. In this study, more than 68% of total Trichoptera species were recorded at coarse substrates; in view of our results, we could identify boulder-pebble and cobble-pebble as target substrates for biomonitoring at patagonian mountainous areas.

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