Distribution of macroinvertebrate assemblages in the Azul-Quemquemtreu river basin, Patagonia, Argentina

M. LAURA MISERENDINO
LINO A. PIZZOLON

  Laboratorio de Ecología Acuática
  Universidad Nacional de la Patagonia
  Sarmiento 849
  9200 Esquel
  Chubut, Argentina
  email: mlau@ar.inter.net

Abstract   Longitudinal and seasonal changes in physical and chemical variables, and macro-invertebrate community structure-function were examined in the Azul-Quemquemtreu river system in the subantarctic forest of Patagonia, Argentina. Patagonian mountain streams have a marked seasonal discharge pattern and may have high suspended sediment loads because of forestry and other land-use practices. The main physical differences among sites were in substrate size (boulder-pebble/sand), mean width (3–37 m), discharge ($<$1–80 m^3 s^{-1}), total alkalinity (275–1210 meq litre^{-1}) and conductivity (31–137 μS cm^{-1}). Species richness and Ephemeroptera, Plecoptera, and Trichoptera richness decreased from upstream sites to the mouth of the river system and were affected by land use. Macroinvertebrate assemblages were influenced by physical (substrate size, width, discharge, current velocity) and chemical (alkalinity and conductivity) variables, and mean density of macroinvertebrates was significantly higher at the Quemquemtreu sites than the Azul sites. Canonical Correspondence Analysis indicated that seasonal trends in macroinvertebrate community composition were related to changes in environmental characteristics of the river, especially water temperature and discharge. The composition of benthic communities in rivers of the Patagonian Andes largely reflect characteristics related to stream size, but factors at the reach scale best explain variation in abundance data. Collector-gatherers were the dominant functional feeding group at all sites. Faunas have similarities with those of New Zealand in taxonomic-functional composition, with a predominance of Chironomidae (Diptera), Leptophlebiidae (Ephemeroptera), and Gripopterygidae (Plecoptera).

INTRODUCTION

Determining the main environmental factors controlling processes and patterns of community structure and function has long been a major goal of stream ecologists. Primary determinants include abiotic factors such as substratum type (Hynes 1970), flow-related factors (Statzner et al. 1988), chemical features (Wright et al. 1984; Ormerod & Edwards 1987), temperature (Ward 1985), and food supply (Vannote et al. 1980), as well as biotic factors such as predation and competition (Lancaster et al. 1988). The River Continuum Concept (RCC, Vannote et al. 1980) provided a framework within which to interpret and predict longitudinal patterns in the macroinvertebrate fauna of river systems using system-wide changes in physical, energetic, and metabolic parameters. However, the predictions of the RCC have not been borne out in all studies where it has been "tested". For example, a paucity or absence of shredders is a characteristic feature of many New Zealand streams, despite substantial inputs of coarse particulate organic matter (Rounick & Winterbourn 1982; Winterbourn 1995). Rivers are characterised by many interacting physical factors that produce spatial and temporal heterogeneity and may exert a major influence on benthic communities (Ward & Stanford 1982; Ward 1989). Hydraulic and substratum conditions in particular have been identified as
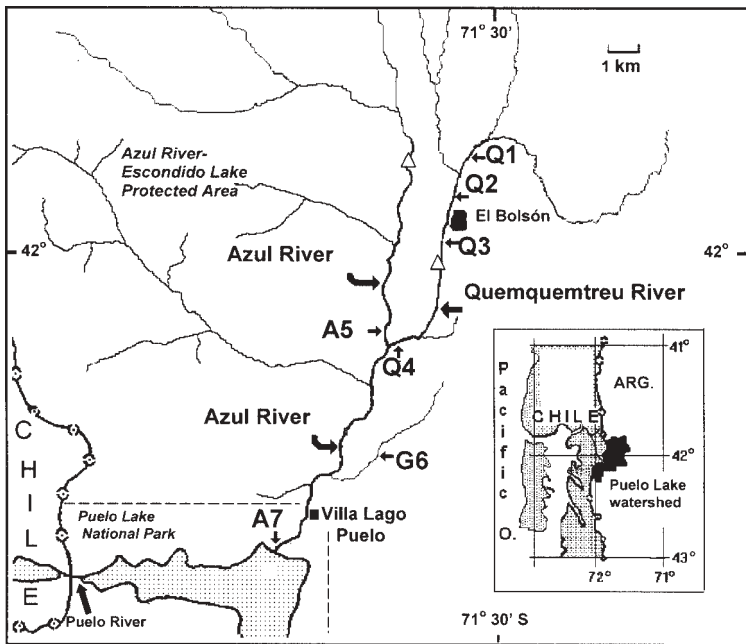
Fig. 1 Map of the Puelo basin area, showing its location in Patagonia, Argentina and the position of sampling sites on the Azul River (A5, A7), Quemquemtreu River (Q1–Q4), and Golondrinas Stream (G6). (Triangles represent the gauging stations.)

physical variables that strongly affect community composition, abundance, and distribution of macroinvertebrates (e.g., Statzner & Higler 1986; Richards et al. 1993).

The macroinvertebrate faunas of rivers and streams in southern South America have received little attention from ecologists until recently (Pratt 1991). The first studies focusing on river macroinvertebates in Patagonia were carried out by Wais (1987, 1990), whereas Miserendino & Pizzolon (2000) investigated the ecology of benthic macroinvertebrates in an organically polluted river system located within a forest-steppe ecotone. Relationships between environmental factors and benthic assemblages at a landscape scale were examined in a more extensive recent study (Miserendino 2001). These and associated studies (e.g., de Cabo & Wais 1991) have resulted in the taxonomic composition of Patagonian stream faunas being fairly well known, but the effects of flow regime and land use on macroinvertebrate assemblages of Patagonian rivers is poorly understood.

In the present study, we analysed patterns of macroinvertebrate community composition, structure, and function at seven sites in a major river basin, in relation to selected chemical and physical variables using a multivariate approach. Our aim was to investigate spatio-temporal patterns in macroinvertebrate faunas at sites representative of a range of physico-chemical conditions, including contrasting situations of discharge and land use, in the Azul-Quemquemtreu river basin. Because the running water fauna of Patagonia shows stronger biogeographic affinities with New Zealand than elsewhere (Boothroyd 2000), and shares several southern families of aquatic insects (Ringuelet 1961; Illies 1969; McLellan 1990; Dominguez et al. 1994) we compare our findings with published New Zealand work.

METHODS

Study area

The Azul-Quemquemtreu basin (1070 km^2) is located on the eastern side of the Andes and discharges into the Pacific Ocean through the Puelo River (Fig. 1). Maximum altitude of the basin is 2200 m a.s.l., and the outlet of the Azul River is at 200 m a.s.l. The rivers studied flow along a tectonic graben covered by sedimentary deposits. The lithology of the Azul is dominated by Mesozoic and Cenozoic granitoids, and mesosilicic vulcanites from the Jurassic and Cretaceous. The Quemquemtreu is dominated by glacio-fluvial deposits from the Holocene. Precambrian crystalline bedrock and granitoids are

also well represented. Quaternary volcanic ashes are widespread. The rivers studied have mainly boulder/ cobble beds, although substratum of the Golondrinas Stream was mixed cobble/sand.

Mean annual air temperature in the basin is 12.1°C, with the mean of the coldest and warmest months being 3.8°C and 17.4°C, respectively (Coronato & del Valle 1988). In the mountains, river discharge is related to rainfall, which occurs mainly in winter, and with snowmelt during spring. Rainfall monitored in the Azul River catchment (1000–2500 mm year^{-1}) is higher than in the catchment of the Quemquemtreu River (<1000 mm year^{-1}) (Fig. 1). Mean annual discharge at the upper Azul River (over 24 years) is 21.8 m^3 s^{-1}, and at the Quemquemtreu River (37 years) is 10.3 m^3 s^{-1} (Agua y Energía Eléctrica 1994). The rivers can be classified as calcium bicarbonate type, since calcium and bicarbonate are the dominant cations and alkalinity is high (Pizzolon 1998).

The study area is located in a region of subantarctic forest. Approximately 47% of the Azul-Quemquemtreu basin is covered in natural forest, of which 30% is native deciduous, 9% native coniferous, and 8% perennial latifoliate forest (mainly *Nothofagus dombeyii*). About 26% of the basin has been modified for agriculture and urban development, or by recent forest fires. The remaining 27% of the basin is high mountain land above the timberline (Pizzolon 1998). In the middle and lower sections of the Quemquemtreu River (sites Q3 and Q4), *Salix fragilis*, an introduced species, is the most common riparian tree. Two urban centers, El Bolsón and Villa Lago Puelo (18 000 and 4500 inhabitants, respectively), are located in the catchment (Fig. 1) but little effluent from these urban centres is discharged directly into the rivers. Tourism, forestry, cattle raising, organic cultivation, and family farming are the dominant economic activities in the catchment and there has recently been growth of small, rural settlements.

Sampling

Seven sampling sites were established within the river system at altitudes between 280 and 450 m a.s.l. Four sites were located in the more developed sub-basin of the Quemquemtreu River and were established to assess possible changes in response to land use and urbanisation. Q1 was in the upper section of the river, Q2 and Q3 were sited either side of El Bolsón city, and Q4 was further down stream. Two sites were located in the Azul sub-basin, which contrasted with the Quemquemtreu sub-basin with respect to discharge

and land use. Site A5 was on the main channel (36.5 km from the source) and A7 was in the lower Azul River 12 km further down. Site G6 was located in a small tributary of the Azul River (Fig. 1).

Substratum composition in each 30 m sampling reach was estimated visually as percentage of boulder, cobble, gravel, pebble, and sand (as defined by Cummins in Ward 1992). Current speed was measured in mid channel on three occasions by timing a float (average of three trials) as it moved over a distance of 10 m (Gordon et al. 1994). Depth was measured in the sampling area using a calibrated stick. Wet ($n = 6$) and dry ($n = 1$) widths of the channel were also determined, and depth was measured during high and low water periods or estimated for large reaches. At each site, air and water temperature were measured with a mercury thermometer. Altitude, distance from the source, and stream order were obtained from IGM maps (Instituto Geográfico Militar 1:100.000).

Discharge was recorded daily by EVARSA (Evaluación de Recursos S.A.) at two sites; one was downstream of Q3 and the other in the upper Azul (Fig. 1).

Water samples for chemical analysis were taken bimonthly from December 1994 to November 1995. Samples were analysed in the laboratory for pH (pH meter/ion analyser Orion 720 SA), conductivity at 20°C (Horiba U2-probe), and total alkalinity (potentiometric titration with two end points). Total nitrogen (TN) and total phosphorus (TP) were determined on unfiltered samples digested with persulphate as described by Pizzolon & Arias (2000).

Quantitative benthic macroinvertebrate samples were taken bimonthly with a Surber sampler (0.09 m^2; 250 µm pore size), from December 1994 to November 1995. However after the flooding, site A7 was inaccessible and could be sampled on only four occasions. On each sampling date, 10 sampling units were collected from each site. They were taken from all habitats according to their abundance within a 30 m reach. The most common habitat types were runs and riffles. Samples were pooled, fixed *in situ* with 4% formaldehyde, and sorted in the laboratory under at least 5× magnification. Macroinvertebrate species were identified using available keys (Illies 1963; Domínguez et al. 1994; Angrisano 1995; Bachmann 1995; Fernández & Domínguez 2001). Total richness and Ephemeroptera, Plecoptera, and Trichoptera (EPT) richness were calculated. Functional feeding groups (FFGs) were assigned by gut content analysis and using available references (Merritt & Cummins 1978; Domínguez et al. 1994;

Albariño & Balseiro 1998; Díaz Villanueva & Albariño 1999).

Data analysis

Community attributes and chemical features of sites were compared using one-way ANOVA (Statistica package 4.5) on log (x+1) transformed data except for pH. Fixed effect ANOVAs were performed using dates as replicates. Significant ANOVAs ($P <$ 0.05) were followed by Tukey honest significant difference (HSD) tests, to identify differences between site means. Associations between abiotic variables and total density, taxon richness, and EPT richness were tested with Spearman rank correlation, incorporating Bonferroni corrections (Rice 1989).

Canonical correspondence analysis (CCA) was used to evaluate relationships between invertebrate communities and environmental variables with the PC-ORD statistical package (version 3.0, McCune & Mefford 1997). CCA is a powerful tool for simplifying complex data sets and, being a direct gradient analysis, it allows integrated analysis of both taxa and environmental data (ter Braak 1986). The technique identifies an environmental basis for community ordination by detecting the patterns of variation in community composition that can be explained best by the environmental variables. Before using CCA, variables that covaried with other measured variables (Pearson correlation coefficient $r>0.65$; $P<0.01$) were removed. Thus, distance from source, stream order, and conductivity were not used in the final ordination. Rare species (<1 % at a sampling site) were not included in the CCA. Additional CCAs were performed using relative abundances of species and presence-absence data. Species-environment correlation coefficients provided a measure of how well variation in community composition could be explained by individual environmental variables. A Monte Carlo permutation test (Jckel 1986) was used to assess the significance of the canonical axes extracted.

RESULTS

Environmental factors

Substrate size was similar at sites Q1–Q3, and A5, and mainly comprised boulders, cobbles, and pebbles (Table 1). At site G6, pebbles and sand were the dominant particle types, and were covered by a species of *Myriophyllum*. Cobbles and gravel were the main substrata at A7. Water temperature ranged from a minimum of 5°C in June to a maximum of 16°C

in March (Table 1). Maximum current velocity recorded was 3.1 m s^{-1} during a flood (Q1) and the minimum was 0.5 m s^{-1} (G6). Mean discharge ranged from 2.0 m^3 s^{-1} in G6 to 37.19 m^3 s^{-1} at A7. Discharge was significantly higher in the Azul than the Quemquemtreu with a peak in June caused by high rainfall and a second lower peak in spring as a result of snowmelt (Fig. 2).

Chemical data provided a clear distinction between the Quemquemtreu sites and those on the Azul River, with conductivity and total alkalinity being significantly higher at the Quemquemtreu sites (ANOVA $F_{(6,35)} = 33.5$, $F_{(6,35)} = 42.9$, $P<0.001$ respectively) (Table 1). Conductivity increased from 72 to 104 μS cm^{-1} from Q2 to Q3, and declined to 82 μS cm^{-1} at Q4. Maximum conductivity recorded from G6 was 20% higher than in the Quemquemtreu. Total alkalinity showed the same pattern as conductivity in the Quemquemtreu, and was highest (969 eq litre^{-1}) at Q3. River water pH was similar at all sites (7.3–7.7). TN and TP concentrations were higher in the Quemquemtreu than in the Azul, however, differences were significant only for TP (ANOVA, $F_{(6,31)} = 8.07$, $P<0.001$). The highest values of TN and TP (140 and 38 μg litre^{-1}, respectively) were observed at Q3, as a result of non-point urban inputs from El Bolsón. TP values recovered to 10 μg litre^{-1} before reaching the mouth of the Quemquemtreu. Quemquemtreu River chemistry strongly affected that of the Azul River, increasing its conductivity and total alkalinity by 28% and its nutrients by 50% (Table 1).

Macroinvertebrate assemblages

Sixty-seven taxa of macroinvertebrates, mainly insects, were identified, with Trichoptera (15), Plecoptera (13), Diptera (20), and Ephemeroptera (8) being the best represented orders (Appendix 1). Numbers of taxa recorded per site on specific dates ranged from 8 (A7) to 32 (Q1). Total species richness varied significantly among sites ($F_{(6,33)} = 5.36$, $P<0.001$, Fig. 3A), and was higher at Q1 and lower at A7 than at all other sites. Differences in species richness among dates (all sites combined) were not significant (ANOVA, $P = 0.91$), however mean total macroinvertebrate density ranged from 454 m^{-2} (A7) to 1640 m^{-2} (A2) (Fig 3C). Sampling sites on the Azul River (A5 and A7) had significantly lower densities than the rest of the sites (ANOVA, $F_{(6,33)} = 9.98$, $P<0.001$). Seasonal patterns of taxon richness and invertebrate density are shown in Fig. 4. Correlation analysis indicated that total density and total taxon richness decreased with discharge

Table 1 Environmental factors measured at seven sampling sites on the Azul-Quemquemtreu Rivers, Patagonia, Argentina. Data are means ± SD derived from bimonthly values. Exceptions are current speed, $n = 3$, discharges at sites Q4, A5, and A7 which are mean annual values, and discharge at G6 which is the mean at base flow ($n = 3$). Different superscript letters in a row show significant differences ($P < 0.05$) indicated by Tukey Honest Significant Difference tests following a significant ANOVA.

Sampling site:	Q1	Q2	Q3	Q4	A5	G6	A7
Features of the reach	Constrained	Unconstrained	Unconstrained	Unconstrained	Constrained	Unconstrained	Unconstrained
Riparian vegetation	Native	Mixed forest-pasture	Salix spp-pasture	Salix spp-pasture	Native	Salix spp-pasture	Mixed
Land use	Forestry	Agriculture	Urban	Agriculture	Native forest	Agriculture	Tourism
Stream order	4	4	4	4	4	2	5
Substrate type	Boulder/cobble	Boulder/cobble	Boulder/cobble	Cobble/pebble	Boulder/cobble	Pebble/sand	Cobble/gravel
Temperature range (°C)	5–16	5–15	8–15	5–15	5–16	8–15	5–14
Distance from the source (km)	29.3	38.8	41.4	45.8	34.5	5.25	46.2
Dry stream width (m)	35	35	35	35	70	15	200
Mean wet width (m) ($n = 6$)	29±5.47	14.33±7	21.5±9.4	25.5±11.3	44.1±12.4	9.66±5.5	37.5±11
Depth (cm) high-low flow	70–30	60–30	45–20	60–20	76–35	60–20	100–30
Mean current speed (m s^{-1})	2.5±0.6	1.3±0.6	0.8±0.1	2.2±0.5	0.7±0.2	0.5±0.1	0.7±0.1
Discharge (m^3 s^{-1})	8.5±1.6 [a]	10.0±2.0 [a]	10.0±2.0 [a]	8.0±3.2 [a]	31.7±16 [b]	2.02±0.66 [c]	52.37±25.8 [b]
pH	7.66±1.09 [a]	7.63±1.12 [a]	7.69±1 [a]	7.71±1.12 [a]	7.31±1.2 [a]	7.7±1.2 [a]	7.5±1.3 [a]
Conductivity (µS cm^{-1})	78±6 [ab]	72±11 [a]	104±28 [bd]	82±11 [ab]	40±6 [c]	118±5 [d]	53±7 [e]
Total alkalinity (eq litre^{-1})	676±26 [ab]	670±134 [a]	968±192 [bd]	770±134 [ab]	334±48 [c]	1188±139 [d]	459±78 [e]
Total nitrogen (µg litre^{-1})	38±32 [abc]	41±21 [abc]	103±37 [a]	80±38 [ac]	10±5 [b]	78±30 [ac]	24±17 [bc]
Total phosphorus (µg litre^{-1})	13±10 [ac]	9±5 [ac]	24±14 [a]	10±4 [ac]	3±3 [b]	4±1 [bc]	4±3 [bc]

(Table 2). Total density also increased with pH, conductivity, and TA. Taxon richness increased with conductivity and TA, and EPT richness increased with TP.

EPT richness decreased significantly from site Q1 to Q2 (Fig. 3B), but sites Q2, Q3, and Q4 had similar values. Site A7 had significantly lower EPT richness than A5 and the Quemquemtreu sites (ANOVA, $F_{(6,33)} = 11.99$, $P<0.001$). Of the insect orders, Plecoptera were very abundant at Q1 but decreased in abundance down stream (Fig. 3C). Gripopterygidae was the best-represented family at all sites, although Austroperlidae and Perlidae were also abundant at Q1 (Appendix 1). Ephemeroptera and Diptera comprised more than 40% of individuals at all sites, and more than 70% at Q2, Q3, Q4, and A7. Leptophlebiidae and Baetidae were the dominant mayfly families, and Chironomidae (especially Orthocladiinae) was the best-represented family of Diptera. Tipulidae were also well represented at sites Q1–Q4, and Athericidae were common at Q1 and A5. Simuliidae were abundant at sites Q1, Q2, and Q4, but Trichoptera were only abundant at Q1. Hydropsychidae was the most abundant trichopteran family at most sites, followed by Leptoceridae and Sericostomatidae. Of the non-insect taxa, Lumbriculidae peaked in abundance at G6 where substrate was finest and was also common in the unconstrained reaches of the Quemquemtreu River (Q3 and Q4). The only crustaceans found were amphipods (Hyalellidae), which were most abundant in G6.

Functional feeding groups

Collector-gatherers were the dominant FFG at all sites (Table 3). The relative abundance of shredders, scrapers, filterers, and predators decreased slightly from Q1 to Q4, whereas the proportion of collector-gatherers increased.

The most abundant collector-gatherers were *Paratrichocladius* spp. (Orthocladiinae) and *Meridialaris* spp. (Leptophlebiidae), which peaked at Q3 and Q4, and *Baetis* sp. (Baetidae), which was most common at Q2. The main scrapers at Q1 were gripopterigids and elmids whereas the gastropod *Chilina patagonica* peaked at G6 (Appendix 1).

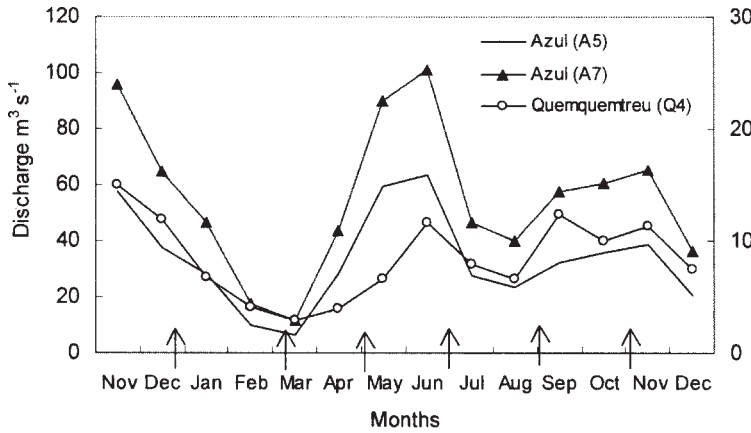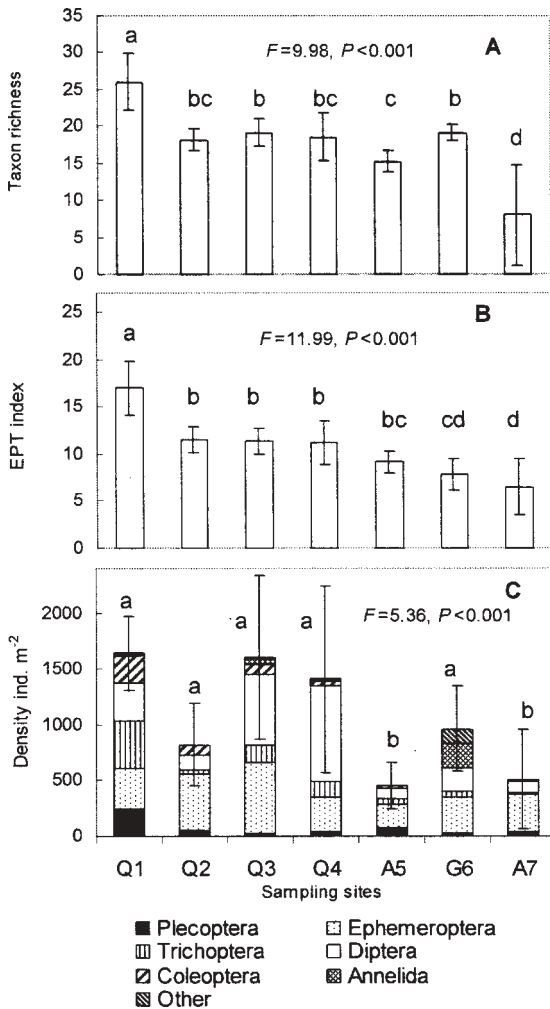The main filterer at Q1 was a hydropsychid, *Smicridea annulicornis*, whereas

Fig. 2 Discharge ($m^3 s^{-1}$) recorded on the Azul (primary y-axis) and Quemquemtreu (secondary y-axis) Rivers during the study period. (Arrows on the x-axis indicate dates when benthos was collected.)

simuliids (*Simulium* sp. and *Gigantodax* sp.) were the main filterers at G6. Predators also had maximum abundance at Q1, where the perlids *Pictetoperla gayi* and *Kempnyella genualis*, a tipulid *Hexatoma* sp., and an athericid *Dasyoma* sp. were common.

Macroinvertebrates and environmental relationships

The CCA ordination showed a good relationship between macroinvertebrate species distribution and measured environmental variables. The strongest explanatory factors were physical and chemical variables, but only 28% of variation in the species abundance data was accounted for by the environmental variables measured (Table 4). The species-environment correlation was >0.81 and an unrestricted Monte Carlo permutation test indicated that all axes were significant. Analyses based on relative abundance and presence-absence data did not increase the explained variance and are not presented. The main environmental gradient (axis 1) was determined by substrate size, width, discharge, and total alkalinity (Fig. 5, Table 5). Samples taken from the Azul and Quemquemtreu Rivers are positioned on the left,

Fig. 3 Mean (±1 SD) **A**, taxon richness; **B**, Ephemeroptera, Plecoptera, and Trichoptera index; and **C**, density of macroinvertebrate groups at seven sites in the Azul-Quemquemtreu catchment ($n = 6$, except A7 $n = 4$). (Superscript letters show significant differences among sites ($P<0.05$) as indicated by Tukey Honest Significant Difference tests.)
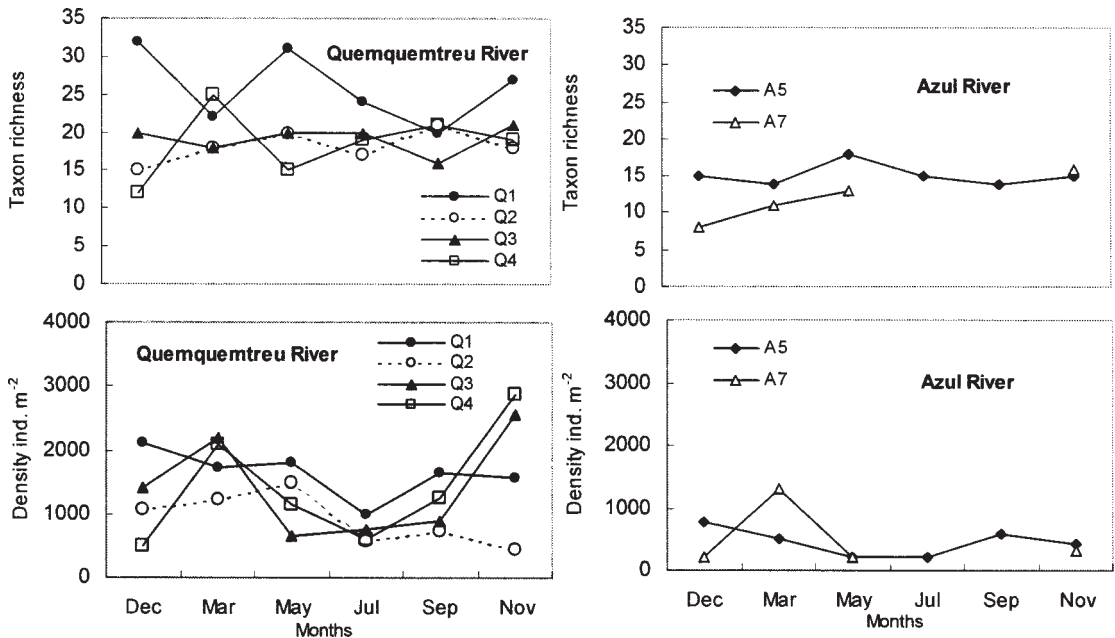
Fig. 4 Bimonthly taxon richness and density of macroinvertebrates at sites Q1–Q4 on the Quemquemtreu River and A5 and A7 on the Azul River, Patagonia, Argentina. Data at site A7 were not available for months July and September.

Table 2 Spearman rank correlations between environmental and biological variables at seven sites on the Quemquemtreu-Azul river system, Patagonia, Argentina. Significant correlations after Bonferroni corrections are shown in bold ($n = 40$; $P<0.05$). (EPT, Ephemeroptera, Plecoptera, and Trichoptera richness.)

Variable	Taxon richness	Total density	EPT index
Discharge	**−0.45**	**−0.41**	−0.23
pH	0.23	**0.43**	0.10
Conductivity	**0.47**	**0.40**	0.16
Total alkalinity	**0.40**	**0.45**	0.07
Total nitrogen	0.26	0.23	0.05
Total phosphorus	0.32	0.35	**0.44**

whereas those from Golondrinas Stream are on the right.

The second environmental gradient was associated mainly with factors that changed seasonally, as shown by strong correlations with temperature, current velocity and discharge. Sites sampled during the high water period or those with highest current velocities and lowest temperatures are located in the bottom left quadrat of Fig. 5. Samples taken during summer are located in the right upper quadrat. Less explanatory power was shown by the third axis, which was correlated with total alkalinity, width, and TP.

DISCUSSION

Insects are the dominant group of macroinvertebrates in Patagonian mountain streams, and most species are endemic to Patagonia (Wais 1990; Miserendino & Pizzolon 2000). In the rivers considered in the present study, Plecoptera, Ephemeroptera, Trichoptera, and Diptera comprised more than 60% of individuals at all sites. The invertebrate faunas of many stony streams in New Zealand and Australia are also dominated by these four orders of insects, with many of the same families prominent (Towns 1979; Lake 1995; Winterbourn 1995). However, Boothroyd

(2000) concluded that the strongest southern affiliations were between New Zealand and South America. Strong affinities between the Patagonian and New Zealand aquatic invertebrate faunas are indicated by their having several southern families in common. They include the Ameletopsidae, Leptophlebiidae (in part), Austroperlidae, Gripopterygidae, Notonemouridae, Hydrobiosidae, Philorheithridae, Helicophidae, and Dugesiidae (Illies 1969; McLellan 1990; Boothroyd 2000). However, several families that are widespread or common in Patagonia are not found in New Zealand and include Perlidae, Baetidae, Glossosomatidae, Limnephilidae, Athericidae, Hyalellidae, and Sericostomatidae. Numerous cosmopolitan families of Annelida, Diptera, Coleoptera, Trichoptera, and Odonata are also present in both regions (Ringuelet 1961).

The trichopteran families Leptoceridae, Hydrobiosidae, and Hydropsychidae were collected throughout the Azul-Quemquemtreu river system, and Sericostomatidae were absent only from the furthest downstream site. Leptophlebiid mayflies were widespread and abundant as they are in stony New Zealand streams, as were Baetidae, which are absent from the New Zealand fauna. Species of Gripopterygidae were the numerically dominant stoneflies as they are in many New Zealand mountain streams where, as in Patagonia, they may co-occur with species of Austroperlidae and Notonemouridae (Winterbourn et al. 1981; Boothroyd 2000).

Lowest taxon richness of macroinvertebrates was recorded at A7. This section of river had the highest discharge, and most substrates were unconsolidated cobbles and gravels. The leptophlebiids *Meridialaris chiloeensis* and *M. diguilina* and a chironomid *Paratrichocladius* sp. were the most common species at site A7 after the flooding, consistent with the findings of Death (1995) that members of these two families (Leptophlebiidae, Chironomidae) are strong colonisers. In late summer, *Limnoperla jaffuelli*, *Baetis* sp., *Elmidae* sp., and *Dasyoma* sp. appeared, possibly in response to more constant stable conditions, greater variety of habitat, and increased food resources.

Macroinvertebrate density was significantly higher in the Quemquemtreu River than at the Azul River sites. This difference between the two rivers can probably be explained by food availability in conjunction with their different discharge regimes. Low invertebrate production can be a consequence of high discharge or low food availability (Wohl et al. 1995; Collier & Winterbourn 1990), and low water hardness was associated with low secondary production by Clenaghan et al. (1998). Nutrients, conductivity, and alkalinity values were significantly

Table 3 Functional feeding groups (FFG) at sampling sites on the Azul-Quemquemtreu river system, Patagonia, Argentina over six sampling occasions combined. Data are percentage of mean relative abundance.

FFG (%)	Q1	Q2	Q3	Q4	A5	G6	A7
Shredders	12.9	6.2	5.5	3.0	14.2	3.6	1.1
Scrapers	17.2	9.5	5.3	5.0	19.9	8.6	9.4
Collector-gatherers	44.4	72.6	80.6	81.2	51.4	79.9	81.8
Collector-filterers	18.4	6.0	5.3	7.8	2.5	3.2	2.0
Predators	7.1	5.8	3.2	3.0	12.0	4.8	5.7

Table 4 Summary of the canonical correspondence analysis (CCA) of quantitative invertebrate and environmental data from the Azul-Quemquemtreu basin, Patagonia, Argentina.

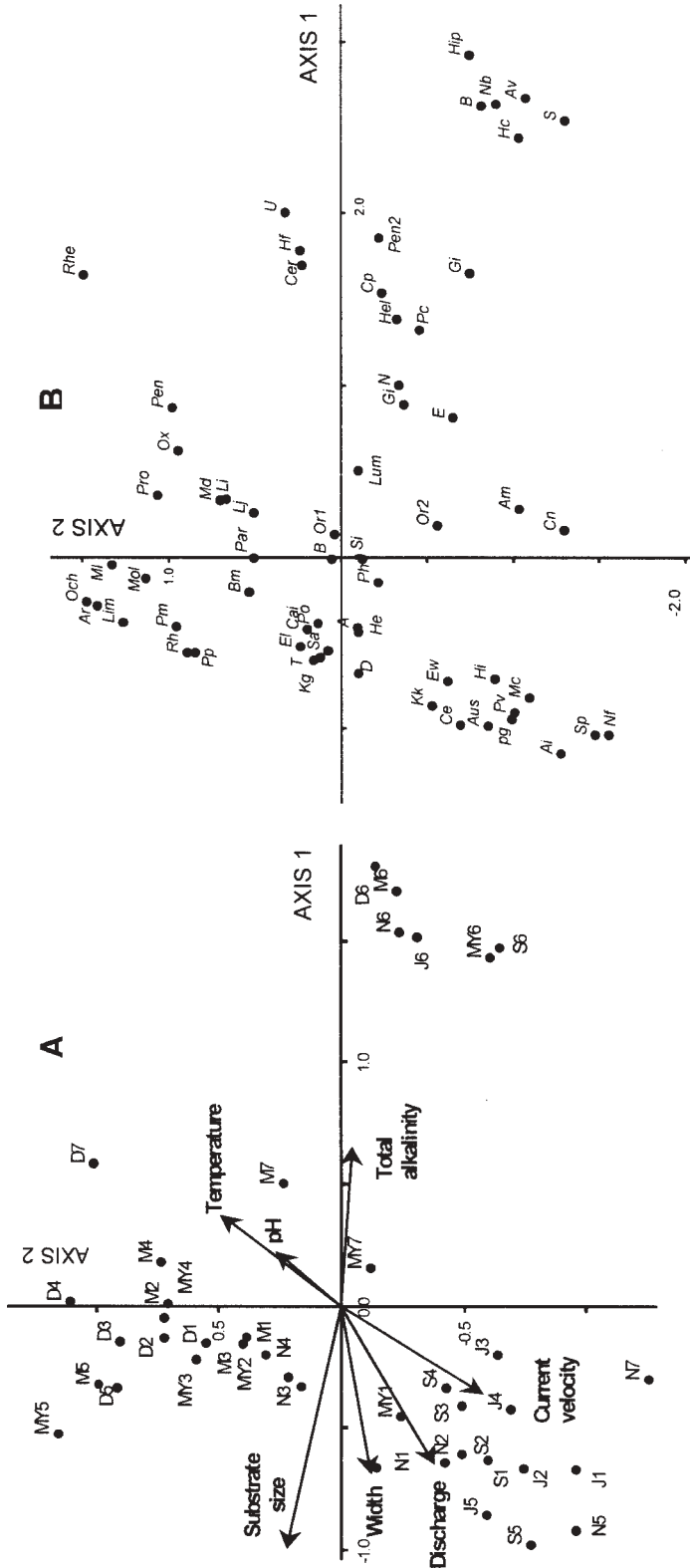| Axes:	1	2	3	Total inertia
Eigenvalues	0.33	0.14	0.09	2.07
Species-environment correlation	0.98	0.90	0.81	
Cumulative percentage variance of species data	16.1	22.9	27.4	
P values for Monte Carlo Permutation test	0.01	0.02	0.01	

Fig. 5 Canonical correspondence analysis (CCA) ordination plots for **A**, sites and environmental variables and **B**, species. Code for species in Appendix 1. (Monthly codes are: D, December; M, March; MY, May; J, July; S, September; and N, Novenber. Sites are: 1, Q1; 2, Q2; 3, Q3; 4, Q4; 5, A5; 6, G6; and 7, A7.)

lower at the Azul River sites than in the Quemquemtreu. Moreover, since density was correlated positively with conductivity and alkalinity, it is likely that inputs of nutrients to the Quemquemtreu enhanced primary productivity, which was reflected by an increase in macroinvertebrate density. Inputs of nutrients can significantly increase secondary production, especially in open-canopied reaches where the main pathway of energy flow is through periphytic production (Zalewsky et al. 1998).

Although sites Q3 and Q4 on the Quemquemtreu River had high average densities, they also had the greatest temporal variation in total density. These sites were located in an unconstrained section of the river where riparian vegetation was dominated by *S. fragilis*, and where a large amount of sediment was deposited as gravel/sand bars after flooding. Sedimentation disrupts benthic stream communities in many parts of the world (Ryan 1991) and releases of suspended solids can affect benthic populations, by reducing total density or augmenting resistant species such as many oligochaetes and chironomids (Gray & Ward 1982). Consistent with this scenario, Lumbriculidae and *Paratrichocladius* spp. were significantly more abundant at sites Q3 and Q4 than elsewhere. The reduction in taxon richness and EPT richness and the absence of some less tolerant taxa to sedimentation from sites Q1–Q3, where native riparian forest is being replaced by introduced tree species and the amount of pasture is increasing, could be a response to land use. Quinn & Hickey (1990) found that New Zealand river catchments with more than 30% of their area in improved pasture had lower taxonomic richness, and lower biomass of Ephemeroptera, Plecoptera, and Trichoptera, and Scarsbrook & Halliday (1999) found that EPT density was significantly greater in native forest than pasture streams in New Zealand.

Only minor contamination was found below the town of El Bolsón on the Quemquemtreu River. Although concentrations of TN and TP were elevated, densities of collector-gatherers increased and taxon diversity declined slightly. Because of its low discharge, Golondrinas Stream had an insignificant impact on the nutrient load of the Azul River.

Our CCA indicated that macroinvertebrates responded to a number of physico-chemical variables. Substrate size and variables related to river size have been found to be important in other Southern Hemisphere studies (e.g., Marchant 1988; Fowler & Death 2000) and in other Patagonian rivers (Miserendino & Pizzolon 2000). We found that specific species assemblages could be predicted in part by substrate size, whereas temporal density variation seems to respond to river flow changes between seasons. We also detected a seasonal trend in macroinvertebrate abundance; correlations with temperature as well as seasonal discharge were significant, and these two variables explained in part the observed temporal patterns in total density and assemblage composition. This is consistent with observations made by Marchant (1988) that numbers of taxa and the mean density of macroinvertebrates increased in summer and decreased in winter in cobble-bed rivers in Australia. Alkalinity and its close correlate conductivity, were also strongly associated with community structure in the Azul-Quemquemtreu as found elsewhere by Wright et al. (1984), Psenner & Catalán (1994), and Zalewski et al. (1998).

Golondrinas Stream was an extreme outlier in our ordination analysis, since it had a very different macroinvertebrate community including large numbers of Lumbriculidae, *Penaphlebia chilensis*, and *Chilina patagonica* that were uncommon at the other sites. It also differed from the rivers in its smaller size, predominance of run-pool habitat, finer

Table 5 Weighted intraset correlation of environmental variables with the axes of canonical correspondence analysis (CCA) in the Azul-Quemquemtreu basin, Patagonia, Argentina.

Variable	Axis 1	Axis 2	Axis 3
Substrate size	**−0.94**	0.26	0.20
Width	**−0.65**	−0.14	**−0.37**
Current velocity	−0.34	**−0.67**	−0.27
Discharge	**−0.51**	**−0.50**	0.03
Water temperature	0.36	**0.58**	0.01
pH	0.22	**0.32**	0.29
Total alkalinity	**0.62**	−0.06	**0.53**
Total nitrogen	0.15	0.25	0.26
Total phosphorus	−0.31	−0.06	0.31

sediments, and extensive patches of the macrophyte *Myriophyllum*. Only 28% of the variation in macroinvertebrate community structure was explained by the ordination, indicating that unmeasured variables such as resource availability (e.g., detritus, peryphyton) and biotic interactions (e.g., predation) could also be important.

The dominant FFG at all our sites was the collector-gatherers, a finding consistent with that of other studies in Patagonia (Wais 1990; Miserendino & Pizzolon 2000). Shredders were not abundant at any site, although nine taxa were classified in this group, a number significantly lower than the 15 reported for the Esquel-Percy system (Miserendino & Pizzolon 2000). Winterbourn et al. (1981) noted an absence or paucity of shredders from many forested mountain streams in New Zealand and proposed that their instability and the unpredictability of high flows were important causative factors leading to leaf litter retention. The paucity of shredders at our sites was more likely due to the sites being located in medium-size streams which do not appear to provide suitable habitat for species of Limnephilidae and Tipulidae, which are common shredders in many smaller streams. A climatic/physical disturbance explanation is less likely since discharge patterns are seasonally predictable (Jobbágy et al. 1995; Paruelo et al. 1998). Nevertheless, the functional organisation of New Zealand and Patagonian mountain streams appears to be very similar, in that both are dominated by collector-gatherers, and related insect taxa play comparable ecological roles in both regions. Large austroperlids and small leptocerids are common shredders in both countries. However in New Zealand, Oeconesidae are a major group with leaf and wood shredding larvae and Conoesucidae rather than Sericostomatidae include detritivores capable of shredding leaves. Collector-gatherers and scrapers (or in the terminology used in New Zealand, collector-browsers) on both land masses are endemic species of Leptophlebiidae, Gripopterygidae, and Chironomidae, whereas filter-feeders are represented by species belonging to the cosmopolitan families Hydropsychidae and Simuliidae. Philopotamidae are also common filter-feeders in New Zealand forest streams but have not been reported from Patagonia (Angrisano 1995). In Patagonia invertebrate predators include species of Hydrobiosidae, Philorheithridae, Glossiphonidae, Dugesiidae (Tricladida), and several groups of Diptera, all of which occur in New Zealand. However, Perlidae and Athericidae are not found in New Zealand, where Corydalidae (Megaloptera) and Eustheniidae (Plecoptera) are the most widespread, large, predatory stream insects. The latter, but not the former, are found in Patagonia but most records are from small, heavily forested streams unlike those considered in the present study (de Cabo & Wais 1991).

Finally, because running waters in the Patagonian mountains are more predictable in terms of discharge than those in New Zealand one might expect the life cycles of stream insects to demonstrate a greater degree of synchrony in growth. Consistent with this prediction, a recent seasonal study indicated that the life cycles of species of Plecoptera are relatively well synchronised (Miserendino 2000). Much more work is needed on the life histories and distributional ecology of Patagonian stream insects so we can better understand the consequences of land degradation and its effects on the integrity and conservation of running waters in Patagonia.

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Appendix 1 Mean annual densities (ind. m^{-2}) of identified taxa at seven sites in the Azul-Quemquemtreu river system, Patagonia, Argentina. (Functional feeding groups (FFGs) assigned: S, shredder; P, predator; Sc, scraper; CG, collector-gatherer; and CF, collector-filterer. CO = code used in Fig. 5.)

			Stations						
	FFG	CO	Q1	Q2	Q3	Q4	A5	G6	A7
Turbellaria									
Dugesiidae									
Girardia sp.	P	Gi	0.3	0	0	0.8	0	7.2	0
Annelida									
Oligochaeta									
Lumbriculidae sp.	CG	Lum	11.3	4.0	44.2	23.8	5.0	219.3	6.0
Hirudinea									
Glossiphoniidae sp.	P	Hel	0.2	0	4.2	0.2	0	4.7	0
Mollusca									
Chilinidae									
Chilina patagonica Sowerby	SC	Cp	5.8	0.3	2.8	0.7	0	95.2	0.3
Planorbidae									
Biomphalaria sp.	SC	B	0	0	0	0	0	1.5	0
Crustacea									
Amphipoda									
Hyalella curvispina Shoemaker	CG	Hc	0.2	0	0	0.2	0	22.8	0
Acari			0	0	0	0.2	0	0	0
Ephemeroptera									
Ameletopsidae									
Chiloporter eatoni Lestage	P	Ce	2.7	0	0.2	0.5	2.2	0	0.3
Baetidae									
Baetis sp.	CG	B	112.8	175.7	124.0	108.5	26.7	114.5	16.3
Leptophlebiidae									
Meridialaris laminata Ulmer	CG	Ml	205.8	193.0	450.3	138.2	88.3	6.8	2.0
M. chiloeensis Demoulin	CG	Mc	28.2	115.3	80.3	60.8	85.7	0	60.5
M. diguilina Ulmer	CG	Md	0	111.0	13.8	0	0	0.8	254.5
Penaphlebia chilensis Eaton	CG	Pc	15.3	3.7	0.5	0.8	0.3	196.0	0.5
P. vinosa Demoulin	CG	Pv	0.5	0	0	0	0	0	0
Nousia bella Pescador & Peter	CG	Nb	0	0	0	0	0	4.7	0
Plecoptera									
Austroperlidae									
Klapopteryx kuscheli Illies	S	Kk	33.7	8.3	1.7	0.2	7.0	0	0.8
Perlidae									
Pictetoperla gayi Pictet	P	Pg	20.8	5.8	0.2	0.3	0.5	0	0
Kempnyela genualis Navás	P	Kg	6.2	2.7	3.7	3.2	3.8	0	0.5
Gripopterygidae									
Notoperlopsis femina Illies	SC	Nf	21.7	0.2	0	0	0	0	0
Antarctoperla sp.	S	A	11.3	5.0	3.5	8.8	3.5	3.7	0
A. michaelseni Klapálek	S	Am	23.0	1.7	9.5	0.3	0	19.0	2.5
Limnoperla jaffueli Navás	SC	Lj	3.8	2.7	1.8	16.7	24.8	6.0	38.0
Aubertoperla illiesi Illies	SC	Ai	116.3	0	1.5	3.0	38.5	0	1.0
Potamoperla myrmidon Mabille	SC	Pm	0.8	0.2	0	0	0.2	0	0
Senzilloides panguipulli Navás	S	Sp	6.7	25.2	0	2.8	0.2	0	0
Pelurgoperla personata Illies	CG	Pp	0.7	0	0.3	0	0	0	0
Chilenoperla puerilis Illies	S		0.3	0	0	0	0	0	0
Notonemouridae									
Udamocercia arumifera Aubert	SC	U	0	0	0	0.3	0	1.0	0
Trichoptera									
Leptoceridae									
Brachysetodes major Schmid	S	Bm	83.5	9.0	45.2	24.8	54.7	4.5	2.0
Hudsonema flamini Navás	S	Hf	2.8	0	0	0	0	4.3	0
Sericostomatidae									
Parasericostoma ovale Schmid	S	Po	19.8	8.3	14.3	3.8	0.3	0.7	0

	FFG	CO	Q1	Q2	Q3	Q4	A5	G6	A7
					Stations				
Hydrobiosidae									
Cailloma sp.	P	Cai	5.3	3.5	7.7	10.8	0.2	0	0.3
Neoatopsyche sp.	P	N	4.5	2.0	2.8	2.5	0	21.7	0
Rheochorema sp.	P	Rh	0.3	1.5	0.8	0.8	0.8	0	0
Australachorema rectispinum Schmid	P	Ar	0	2.8	0	0	0	0	0
Hydropsychidae									
Smicridea annulicornis Blanchard	CF	Sa	303.3	22.5	86.5	104.8	2.0	0	5.8
Philorheithridae	P	Ph	0.8	0.2	0.7	0	0.2	0.2	0
Glossosomatidae									
Mastigoptila sp.	SC		0.2	0.2	0	0	0	0	0
Limnephilidae	S	Li	0.8	0.3	0.8	0.2	0.2	1.2	0
Hydroptilidae									
Hydroptilidae sp	SC	Hip	0	0	0	0	0	16.2	0
Oxyethira bidentata	SC	Ox	0.2	0	0	0	0.2	0.2	0
Ochotrichia sp.	SC	Och	1.0	0	0	0	0	0	0
Helicophidae									
Eosericostoma sp.	SC		0.2	0	0	0	0	0	0
Diptera									
Chironomidae									
Paratrichocladius sp. 1	CG	Par	129.8	31.3	203.0	243.7	31.3	30	19.3
Paratrichocladius sp. 2	CG	Or1	124.3	48.7	179.8	531.0	3.0	129.2	22.5
Orthocladiinae sp. 1	CG	Or2	5.0	0.5	3.7	4.3	0.7	2.3	6.3
Orthocladiinae sp. 2	CG	Pro	0	4.2	0	2.0	0	1.2	6.8
Pentaneurini sp.	CG	Pen	0.2	0.2	2.5	16.3	0	4.2	22.5
Pentaneura sp.	CG	Pen2	0	0	1.2	0	0	8.5	1.3
Rheotanytarsus sp.	CG	Rhe	0	0	0	0	0	0.3	3.0
Simuliidae									
Simulium sp.	CF	Si	13.5	11.0	7.2	4.7	4.7	10.2	4.3
Gigantodax sp.	CF	Gi	0.7	0	0	1.8	0.3	20	0
Cnesia sp.	CF	Cn	0.2	0	2.7	0	0	0.2	0
Tipulidae									
Hexatoma sp.	P	He	17.2	19.5	16.7	19.0	1.7	0.3	7.0
Limnophila sp.	P	Lim	0.7	12.5	0.2	0	0	0	0
Molophilus sp.	P	Mol	1.0	0.8	0	1.2	0.7	0.3	0
Athericidae									
Dasyoma sp.	P	D	39.8	4.7	6.7	0.8	46.7	0	19.0
Empididae	P	E	0.3	0	0.5	0.2	0	1.3	1.3
Muscidae									
Lispoides sp.	P		0	0	0	0.2	0.2	0	
Syrphidae	P	S	0	0	0	0	0	0.5	0
Ceratopogonidae	P	Cer	0.7	0	0	0	0	1.0	0
Tabanidae	P	T	2.0	0	0	2.3	0.2	0	0.3
Blephariceridae									
Edwardsina sp.	SC	E	0.2	1.8	0.2	0.5	0	0	0.3
Coleoptera									
Elmidae									
Elmidae sp.	SC	El	252.2	83.8	84.2	34.3	19.5	0.2	7.5
Austrelmis sp.	SC	Aus	1.8	0	0	0	0	0	0
Odonata									
Aeshnidae									
Aeshna variegata Fabricius	P	Av	0	0	0	0	0	8.2	0