

Seasonal patterns of benthic arthropods in a subtropical Andean basin

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Abstract

We studied the seasonal variation of arthropod assemblages and the response to high discharge events in a subtropical Andean basin. Using abundance of common taxa and taxon richness of each sampled site, we examined the temporal variation of arthropods and related these changes with 12 environmental variables. Seasonal patterns of benthic arthropods were confirmed by uni- and multivariate techniques. Benthic abundance and taxon richness peaked on autumn-winter months, and declined abruptly on the month of peak discharge (summer season). Distinct taxonomic groups were dominant in each season influenced by discharge and seven chemical variables.

Assemblage resistance to disturbance by spates was low. Rapid recovery of benthic arthropods after floods reflected high resilience of the system. The dominance of groups of short life cycles such as Ephemeroptera played an important role in this process.

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Introduction

In aquatic systems, one of the primary potential agents of disturbance is flooding (Hendricks et al., 1995). Resh et al. (1988) are quite insistent in that floods impact structural and functional components of stream biota and may play a role in the evolution of these organisms. The effects of spates have been measured in terms of resistance and resilience, which together provide an index of the ecological stability of stream ecosystems (Grimm and Fisher, 1989; Boulton et al., 1992; Golladay, et al. 1992). Recovery from disturbances has been defined as the reestablishment of community structure or function to pre-disturbance conditions (Wallace, 1990). It is facilitated by the

dispersal of surviving individual inhabiting refuge such as the hyporheic zone (Brooks and Boulton, 1991), by downstream drift (Williams and Hynes, 1976) or by aerially ovipositing adults (Gray and Fisher, 1981).

Variability and seasonality in precipitation are the principal defining attributes of monsoon climate (Minetti and Poblete, 2003), and the resulting hydrology influences the structure of stream communities (Resh et al., 1988).

Our main objective was to examine whether temporal dynamics of arthropod assemblages was related with seasonal variation of precipitation in monsoon-climate streams. In particular, we sought to discover (1) the temporal patterns in abundance and richness of arthropods assemblages, (2) whether these patterns are related with seasonality in rainfall, (3) how arthropods respond to high discharge events in terms of resistance and resilience, and (4) the main environmental variables associated with annual arthropods variation.

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Study area

Lules River Basin (Lrb) ($26^{\circ}36'S$, $65^{\circ}45'W$) is located in the northwestern of Argentina (Tucumán province, Fig. 1), a subtropical region influenced by a monsoon climate. Average annual rainfall (39 years of records) for Obispo Colombres, the closest meteorological station of the study area, is 1141 mm. Nearly all precipitation events occur during 5 months from November to April (summer months, wet season). The average maximum precipitation and discharge are related with January, with values of 226 mm and $20 \text{ m}^3/\text{s}$, respectively. The dry period extends from April to October (autumn/winter season), with minimum average values of rainfall (11.8 mm) and current ($4.64 \text{ m}^3/\text{s}$) on August (data recorded by Obispo Colombres meteorological station of Tucumán province, period 1961–1990).

Bi-monthly variation of precipitation and discharge for the period 1998–1999 is shown in Fig. 2. These data were recorded for Recursos Hídricos office, the gauging station of Tucumán province located near the Ju sampled site. Meteorological data for same period indicated an average air minimum temperature of 12°C in July, and a maximum temperature of 25.5°C in January.

Yungas phytogeographical province, a mountain rain-forest, covers almost all the watershed. This highly diverse forest extends in Argentina between 22°S and 28°S covering 3,900,000 ha (Brown, 2000). A protected area of Yungas (San Javier Park, San Javier hills, Fig. 1) is included in Lrb. San Javier Park covers 14,000 ha and it is administered by the National University of Tucumán.

Elevation ranges from 4488 m.a.s.l. in the northwest of the basin to 408 m.a.s.l. in the southeast (Mesa, 2006). The seasonally high rainfall coupled with this steep gradient and the progressive logging produce high discharge events, scour, sediment deposition and re-arrangement in streams (Mesa, 2006).

Methods

Four sampling sites were selected: Hoyada (Ho), Juntas (Ju), Lules (Lu) and San Javier (SJ) (Fig. 1). The first three sites are located in the main river of the basin

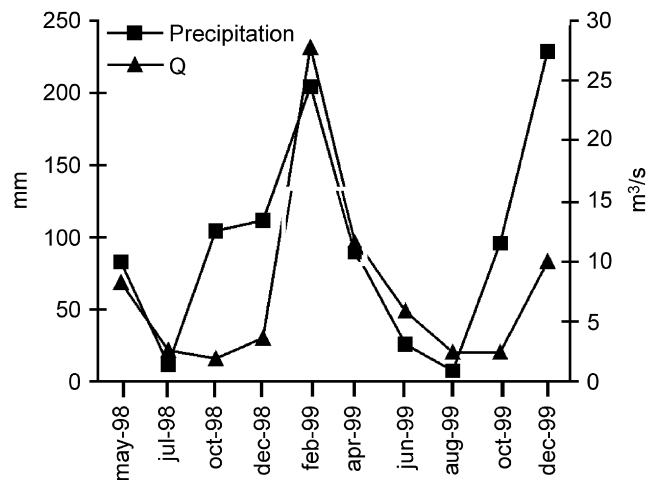


Fig. 2. Bi-monthly variation of precipitation and discharge (Q) during the period 1998–1999.

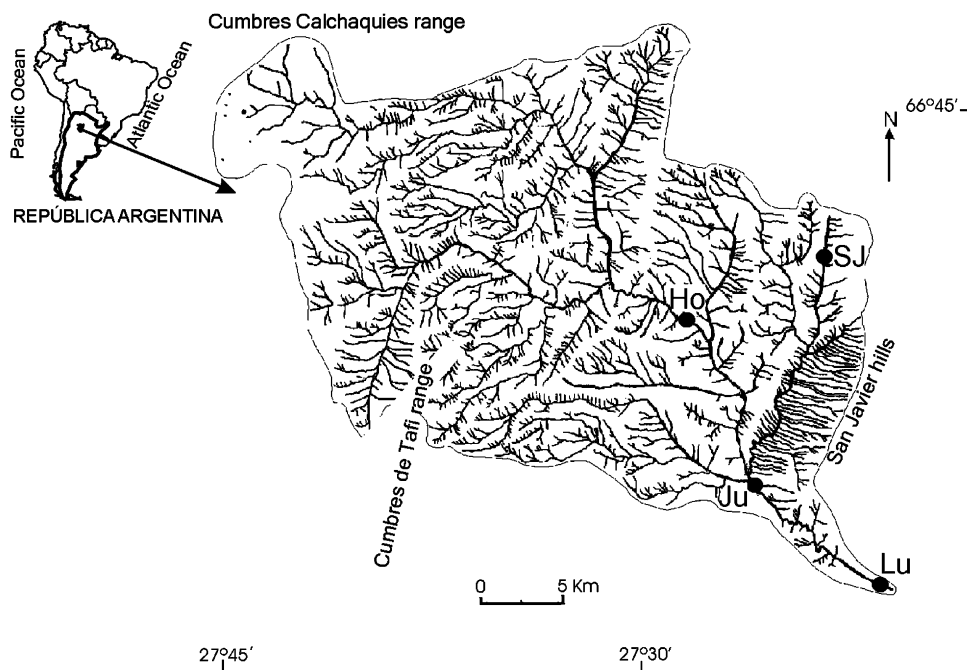


Fig. 1. Map of Lules River Basin showing physiographic units, drainage density and sampled sites: Ho = Hoyada, Ju = Juntas, Lu = Lules, SJ = San Javier.

at different altitudes (seventh-order stream, Fig. 1), while SJ site is situated in a fourth-order stream (Mesa, 2006).

Samples were collected from May 1998 to December 1999 every 2 months. Benthic data of Lu on August 1999 were not included in the analysis due to lack of information.

Three (replicates) invertebrate samples were taken at each station every 2 months using a Surber sampler (300 μ m mesh). The samples were preserved in 4% formaldehyde prior to transportation to the laboratory for processing. Insect orders Trichoptera, Ephemeroptera, Coleoptera and Acari Prostigmata were identified up to the smallest possible taxonomic level. Larvae and adults of Coleoptera were counted and only watermites adults were considered. The replicates were averaged for the analysis.

Dissolved oxygen (DO) and conductivity (COND) were measured *in situ* using the Winkler method (APHA, 1992) and a pocket conductivity meter (Mettrom E587), respectively. Additional water samples were collected for subsequent analysis of total solids (TS), major ions (Na^+ , Mg^{2+} , SO_4^{2-} , Ca^{2+} , K^+ , Cl^-) and nutrients (PO_4^{3-} and NO_3^-). These analyses were made in the laboratory using standard methods (APHA, 1992). Discharge (Q) was assessed with velocity by the flow method and cross-sectional area (Gore, 1996).

Temporal variation in abundance of common taxa (abundance >1%), taxon richness (number of taxa, S) and Q were examined by plotting these variables for each sampled month among sites. The data of Q used in this analysis correspond to that collected on the gauging station of Recursos Hídricos office in each sampled date (Fig. 2).

To examine bi-monthly variation of arthropod abundance within each sampled site, parametric testing could not be used because of the lack of normality (Shapiro–Wilks test, $P < 0.05$). Thus, we used Kruskal–Wallis one-way analyses of variance (Zar, 1996).

Multivariate ordination techniques were applied to analyze the seasonal variability in assemblage composition and to identify the relations between environmental and biological data, using CANOCO 3.0 software (ter Braak and Šmilauer, 1998). Seasonal variation in arthropod assemblages was analyzed by performing a correspondence analysis (CA). CA fits non-linear responses of species to intermediate-to-long underlying multivariate gradients (ter Braak and Šmilauer, 1998). Gradient length is measured axis-wise in standard deviation units of species turnover (SD – Hill and Gauch, 1980; ter Braak and Šmilauer, 1998). Data displaying very short gradients (<1.5 SD) are best analyzed with linear methods such as principal components (ter Braak and Prentice, 1988), whereas in gradients of about 4 SD or longer most of the species responses are likely to be unimodal. In the studied data set, gradient lengths were intermediate (2.1 and 2.8 SD for the first and second axes, respectively). For such

lengths, linear and unimodal methods may be both applicable (ter Braak and Verdonschot, 1995). However, CA is more appropriate when data are counts (ter Braak and Šmilauer, 1998). Rare taxa (abundance <1%) were discarded to reduce the noise (*sensu* Gauch, 1982). Many studies have shown that most information of community structure can be derived from common taxa (reviewed in Gauch, 1982; Marchant, 1990).

Mantel's test with 999 permutations (Mainly, 1997) was used to test the relationship between the species scores of the selected axis of CA with physicochemical and hydrological variables. The values of discharge used in this case correspond to data recollected in the field by the Gore method (Gore, 1996). If the null hypothesis of no correlation between the two sets of distance values is correct, then the value of the test statistic for the observed data would not be in the upper tail (5%) of the distribution of values calculated from the randomly permuted data (Mainly, 1997). Although Mantel's test makes no assumptions about the distribution of the variables the test assumes a linear relationship or at least monotonic between the two variables (Mainly, 1997).

The relation between environmental and biological data was also explored by canonical correspondence analysis (CCA). CCA constrains the CA axes to be linear combinations of the environmental variables (ter Braak and Šmilauer, 1998). Selection of variables was based on stepwise multiple regressions, and the statistical significance of the variables added to the analysis was proved using a Monte Carlo permutation test (9999 unrestricted permutations) (ter Braak and Verdonschot, 1995). Significance was expressed as a P -value, equal to the number of permuted values greater than the observed statistic plus one and divided by the number of permutations plus one. A P -value of 0.01 or less was taken as significantly different from random. Monte Carlo permutations were also used to test whether environmental variables were individually significant. Twelve environmental variables were available; many were highly correlated and could severely distort the ordering of objects in CCA. A forward stepwise selection (ter Braak and Šmilauer, 1998) was used to assemble the final model of environmental variables. Variables were tested one at a time and added to the model (if significant) in order of amount of variation in arthropod data that they explained. Selection stopped when there was no significant increase in variance explained.

Results

Arthropod assemblages structure

A total of 19,287 invertebrates were collected and 63 arthropods taxa identified (Appendix A): 40 taxa (7181 individuals) in Ho, 36 taxa (3300 individuals) in Ju, 30

taxa (3560 individuals) in Lu and 49 taxa (5252 individuals) in SJ. Common taxa were represented by mayfly genera as *Baetodes* spp., *Camelobaetidium penai*, *Varipes* (*minutus* + *singuil*), *Leptohyphes eximius*, *Thraulodes* sp., *Americabaetis albus* and *Nanomis galera*; one riffle beetle (*Austrelmis* sp. larvae and adult); three caddisflies (*Mortoniella* sp., *Smicridea* sp. and *Metrichia* sp.); and one watermite specie (*Torrenticola columbiana*). The three dominant species accounted for about 60% of the total average abundance per sampled site. *Baetodes* spp. was dominant in Ho (45%), SJ (55%) and Lu (28%), *Austrelmis* sp. (larvae) in Ju, Lu (25%) and Ho (17%), and *Leptohyphes eximius* in Ju (23%). The percentage contribution of each order as the sum of the relative abundance of all taxa of each order across all sampled months is shown in Fig. 3. Ephemeroptera was the dominant order in all sampled sites (abundance >50%) (Fig. 3). Also, bi-monthly variation in arthropod abundance was significantly different in all sampled sites (Kruskal–Wallis test, $P < 0.05$) (Table 1).

Temporal variations of benthic arthropods

Bi-monthly variation of arthropods abundance and taxon richness varied in an inversely proportional way with Q (Figs. 4 and 5). In general, abundance peaks in June (1999), July (1998), October (1998–99) and December (1998) (Fig. 4). The abundance of *Austrelmis* sp. (adults) was higher in April (1999) in Ho and Lu (Fig. 4A and B). Richness and abundance declined abruptly on peak discharge, indicating little resistance of

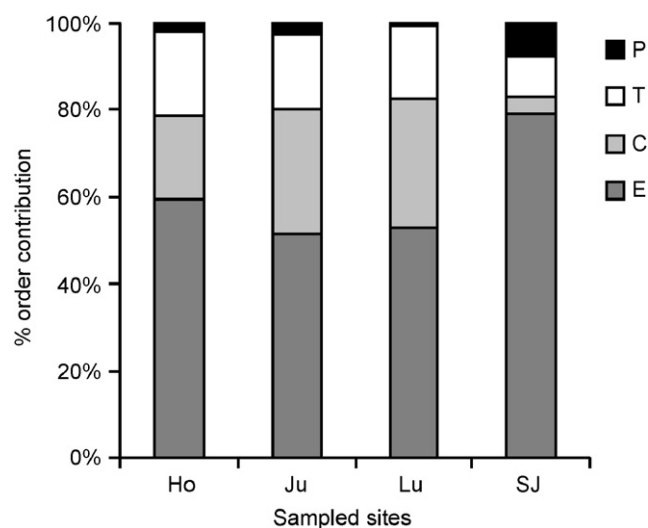


Fig. 3. Percentage contribution of each arthropod order as the sum of the relative abundance taxa of each order across all sampling dates. Ho = Hoyada, Ju = Juntas, Lu = Lules, SJ = San Javier, P = Prostigmata, T = Trichoptera, C = Coleoptera, E = Ephemeroptera.

Table 1. Summary of the non-parametric analysis of variance (Kruskal–Wallis test) used to examine differences in bi-monthly abundance of arthropods per sampled site

Sampled site	df	H	P
Ho	9	26.57	0.0002*
Ju	9	29.46	<0.0001*
Lu	8	18.11	0.0072*
SJ	9	52.48	<0.0001*

Ho = Hoyada, Ju = Juntas, Lu = Lules, SJ = San Javier.

*Probability $P < 0.05$.

arthropod assemblages to spates. This effect was quickly ameliorated by highly resilient groups that recovered rapidly to the pre-disturbance abundance (Figs. 4 and 5).

Ordination analysis

The first three axes of CA explained most (55%) of the total arthropod variation (total inertia 1.9). A broad seasonal variation in arthropod assemblages was evident on the first two axis: autumn–winter samples appeared on the negative side of axis 1 and spring samples on the positive side; summer samples in the positive side of the axis 2 vs. autumn samples in the negative side (Fig. 6A). On axis 1, autumn–winter dominants included *Baetodes* spp. and *Camelobaetidium penai* (Fig. 6B), while *Mortoniella* sp., *Austrelmis* sp. (larvae), *Varipes* sp. and *Metrichia* sp. were most common in spring season. On axis 2, autumn dominants included *Austrelmis* sp. (adults), while *Leptohyphes eximius* was strongly associated with summer samples. Other taxa such as *Torrenticola columbiana*, *Thraulodes* sp. and *Nanomis galera* were also associated with summer season.

On an indirect-gradient basis, ordination scores on CA axis 1 correlated negatively with DO, Mg^{2+} , Na^+ , SO_4 and Ca^{2+} (Table 2). Axis 2 scores correlated positively with Ca^{2+} and K^+ , and negatively with PO_4^{3-} (Table 2). On a direct-gradient basis, the constrained ordination (CCA) of species abundance with stepwise forward selection of environmental variables retained only two variables ($P < 0.01$): SO_4 and Q (Table 3).

Discussion

In this study, we demonstrated the seasonality of benthic arthropods of Lrb. Also, we established the rapid recovery of benthic fauna following high discharge events. In explaining these results, we considered the seasonal variability of taxonomic composition, abundance

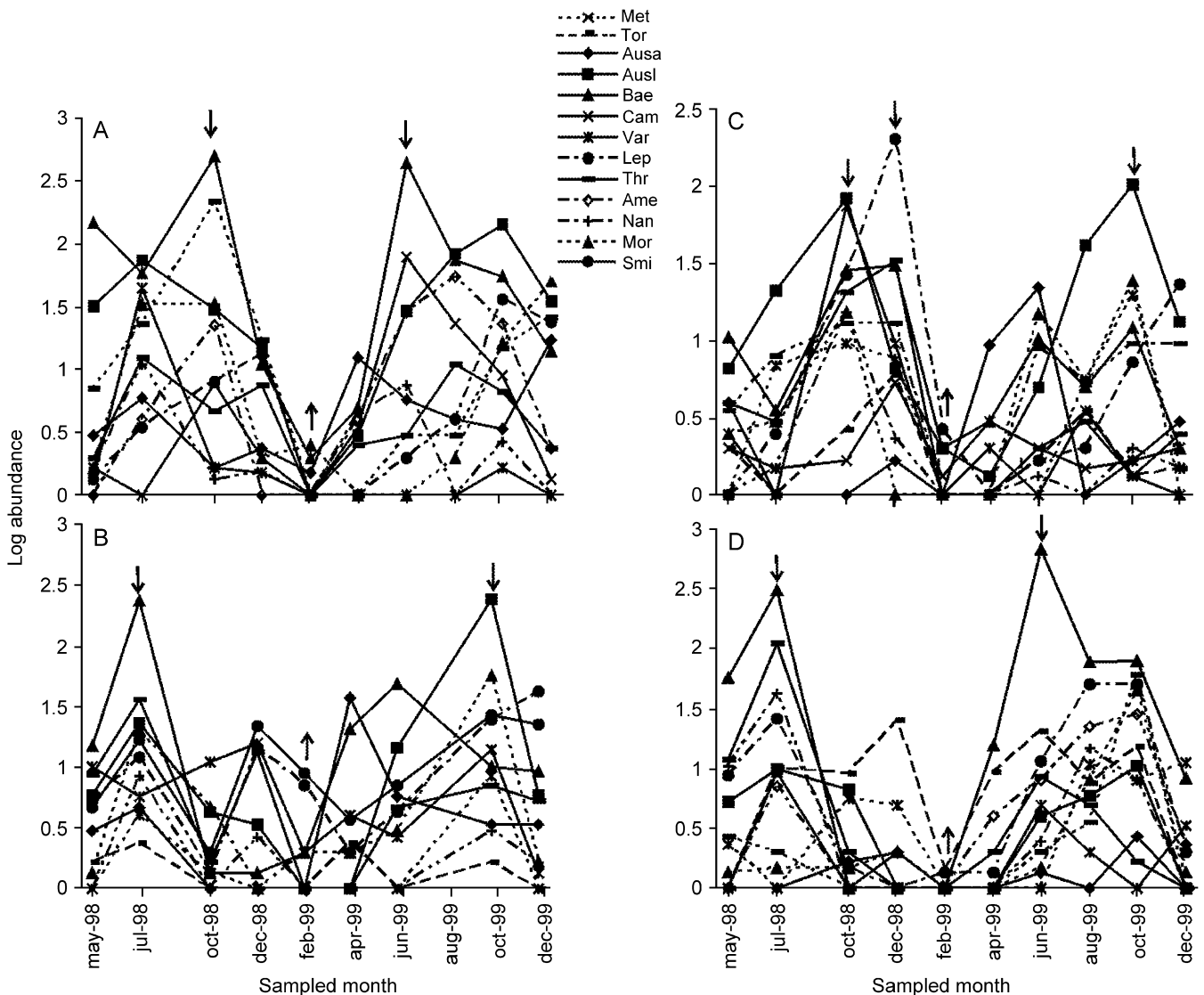


Fig. 4. Temporal changes of arthropods abundance per sampled site: (A) Ho = Hoyada, (B) Lu = Lules, (C) Ju = Juntas and (D) SJ = San Javier. Downward and upward arrows indicate minimum and maximum levels of discharge in the period 1998–1999 (data collected in the gauging station of Recursos Hídricos office, Tucumán, Argentina). Taxa abbreviations: Met = *Metrichia* sp.; Tor = *Torrenicola columbiana*; AUSA = *Austrelmis* sp. (adult); AUSL = *Austrelmis* sp. (larvae); Bae = *Baetodes* spp.; Cam = *Camelobaetis penai*; Var = *Varipes* sp. (*minutus+singuil*); Lep = *Leptohyphes eximius*; Thr = *Thraulodes* sp.; Ame = *Americabaetis alphus*; Nan = *Nanomis galera*; Mor = *Mortoniella* sp.; Smi = *Smicridea* sp. Some taxa were eliminated to clarify the graph.

and taxon richness, and the interpretation of these patterns in relation to physicochemical and hydrological variables.

Temporal variation in abundance and richness of arthropods

The abundance and richness of benthic arthropods of Lrb exhibited a similar bi-monthly variation (Figs. 4 and 5). With one exception, the peaks of abundance and richness occurred in the dry season (Figs. 4 and 5). During December 1998 the levels of discharge were still low as the

rainy season was just beginning (Fig. 2). Arthropod assemblages showed low resistance to summer spates: the peak of *Q* resulted in an abrupt decline of abundance and richness of benthic arthropods (Figs. 4 and 5). Many authors observed similar results around the world in temperate and tropical climates (Pierce, 1986; McElravy et al., 1989; Scrimgeour and Winterbourn, 1989; Flecker and Feifarek, 1994; Jacobsen and Encalada, 1998; Weigel et al., 2003). However, the abundance of *Leptohyphes eximius* and *Smicridea* sp. remained almost constant in the Lu sample site (Fig. 4B). Lu is affected by human actions: flood control levees and channelization of the river

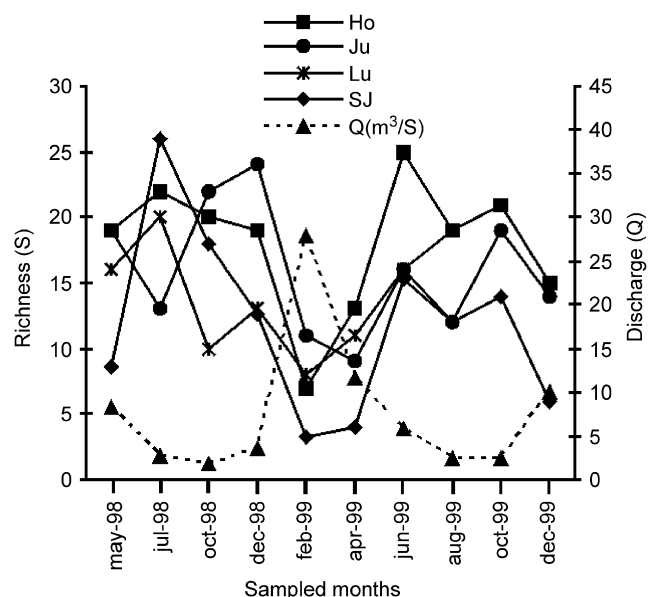


Fig. 5. Bi-monthly variation of taxon richness (number of taxa) and discharge (Q) within the four sampled sites: Ho = Hoyada, Ju = Juntas, Lu = Lules, SJ = San Javier. The values of discharge correspond to data collected in the gauging station of Recursos Hídricos office (Tucumán, Argentina).

changed its geomorphology, altering the disturbance effect. Thus, during the high discharge period, abundance was dominated by these two taxa that were benefited by the new condition.

Rapid recovery after summer spates suggests high resilience of arthropod assemblages of Lrb (Figs. 4 and 5). Aerial recolonization was probably an important source of recruitment, given the high resilience of perennial stream populations and the presence of a protected area within the study basin. Ephemeroptera is an important group in connection with this role. Life-history strategies of mayflies such as short life cycles and continuous emergence ensure rapid recolonization of streams. Another source of potential colonization is possibly the hyporheic zone. The use of the hyporheic zone as a refuge by benthic fauna has been observed in several studies around the world (Sedell et al., 1990; Dole-Oliver et al., 1997; del Rosario and Resh, 2000) and in a local study (Fernández and Palacios, 1989), suggesting that refuge-seeking behavior of arthropods could also play an important role in faunal recovery of Lrb.

Seasonal patterns in arthropod assemblages and related environmental variables

Multivariate analysis reflected the seasonal patterns of arthropod assemblages (Fig. 6) and the importance of

discharge in this ordination (Table 3). Similar patterns have been found in many other regions of the world across different climates (e.g. Boulton et al., 1992; Flecker and Feifarek, 1994; Robinson et al., 2001; Snook and Milner, 2002; Bêche et al., 2006). The increase of *Baetodes* spp. and *Camelobaetidioides penai* during winter–autumn season have been attributed to the extension of life cycles (C. Nieto, personal communication) and the congregating effect of individuals in ever-diminishing habitats (Smith and Pearson, 1987). Physicochemical conditions shifted rapidly during this season. Lower water levels and temperature caused the increase of concentration of some ions like Mg^{2+} , Na^+ , SO_4^{2-} , Ca^{2+} and DO, explaining the variation on axis 1 (Table 2). Two ions (Ca^{2+} , K^+) and a nutrient (PO_4^{3-}) explained the variation of axis 2 (Table 2). The concentration of Ca^{2+} and K^+ was higher during summer months (Table 2). In this season, discharge increases the erosion of rocks, allowing the lixiviation of these ions. The increase of PO_4^{3-} during autumn season could be related with land use. Lrb has important sectors perturbed by anthropic activities (logging, exotic forest and farming) that could affect the natural physicochemistry of streams (Fernández and Molineri, 2006). Besides, *Leptohyphes eximius* and also *Torrenticola columbiana*, *Thraulodes* sp. and *Nanomis galera* are likely tolerant to high discharge levels (summer samples). The abundance increase of Leptophlebiids during floods had been reported by several authors (Nolte et al., 1997; Olsen and Townsend, 2005). In addition, before the wet season, Leptophlebiids may migrate into wetted interstitial substrates that provide refuge (Fowler, 2004).

Many studies have shown the influence of disturbance on the underlying food-base of benthic invertebrates (Resh et al., 1988; Negishi and Richardson, 2006). In addition, taxa could be associated with each season in relation with their food requirements. *Torrenticola columbiana* feeds preferentially upon insect larvae (mainly Diptera) and insect eggs (Di Sabatino et al., 2002), abundant food resources in the summer season in subtropical environments. Besides, caddisflies such as *Mortoniella* sp. and *Metrichia* sp. are specialized in feeding on the uppermost exposed surfaces of rocks where they graze on diatoms and green algae (Wiggins, 1998). Among beetles, some Elmidae species feed on the periphyton of surfaces of rocks and some are detritivorous (especially larvae) (Merritt and Cummins, 1996; Cummins et al., 2005). Also, individuals of *Austrelmis* sp. were found associated with the biofilm of rocks (Archangelsky, 2001). Several local studies had shown the increase of abundance and diversity of algae during spring (Mirande, 2001), explaining the preference of these taxa with this season. Also, the association of *Varipes* with spring would be related with moderate levels of temperature and flow (C. Nieto, personal

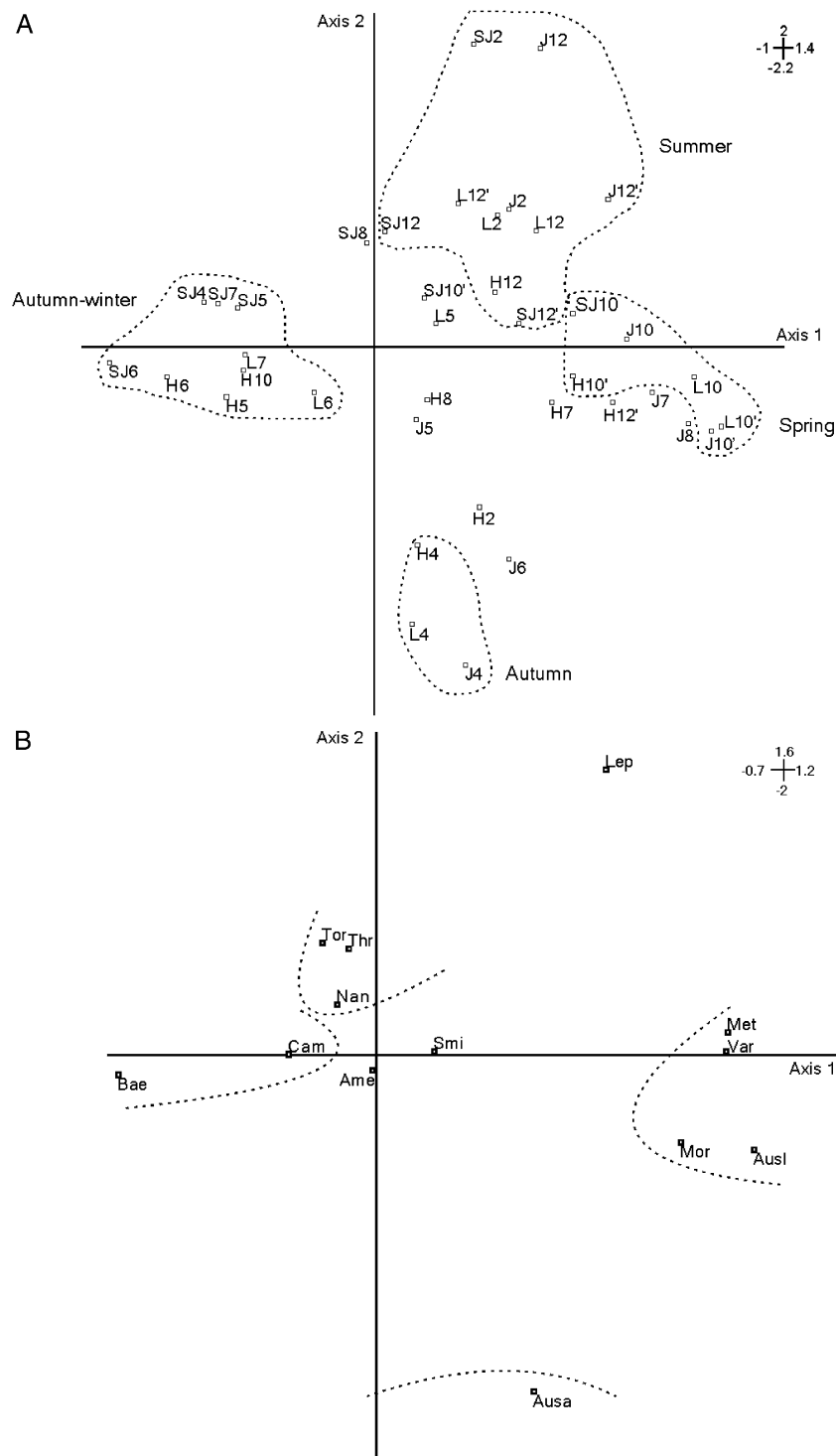


Fig. 6. Correspondence analysis of arthropod assemblages at four studied sites. Curves enclose main recognized groups. (A) Bi-monthly sampled sites. Abbreviations: Ho = Hoyada, Ju = Juntas, Lu = Lules, SJ = San Javier, 5 = May 1998, 7 = July 1998, 10 = October 1998, 12 = December 1998, 2 = February 1999, 4 = April 1999, 6 = June 1999, 8 = August 1999, 10' = October 1999, 12' = December 1999. (B) Species ordination. Met = *Metrichia* sp.; Tor = *Torrenticola columbiana*; AUSA = *Austrelmis* sp. (adult); Ausl = *Austrelmis* sp. (larvae); Bae = *Baetodes* spp.; Cam = *Camelobaetis penai*; Var = *Varipes* sp. (*minutus*+*singuil*); Lep = *Leptohyphes eximius*; Thr = *Thraulodes* sp.; Ame = *Americabaetis alphus*; Nan = *Nanomis galera*; Mor = *Mortoniella* sp.; Smi = *Smicridea* sp.

Table 2. Results of correlation analysis between the species scores of axis 1 and 2 of CA and 12 variables

Variables	Axis 1		Axis 2	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
DO	−0.59	0.04*	−0.30	0.21
TS	0.29	0.18	0.36	0.17
COND	−0.51	0.08	−0.13	0.35
<i>Q</i>	0.56	0.06	0.13	0.34
Mg ²⁺	−0.65	0.01*	0.48	0.10
Na ⁺	−0.70	0.01*	0.48	0.09
SO ₄ ^{2−}	−0.80	0.00*	0.55	0.07
Ca ²⁺	−0.60	0.00*	0.61	0.04*
K ⁺	−0.49	0.08	0.67	0.02*
Cl [−]	−0.48	0.08	0.37	0.15
PO ₄ ^{3−}	−0.04	0.45	−0.67	0.01*
NO ₃ [−]	0.03	0.48	0.42	0.14

DO = dissolved oxygen; TS = total solids; COND = conductivity; *Q* = discharge.

*Significant *P*-values (Mantel's test, *P* < 0.05).

Table 3. Explained variation of species data by individual environmental variables using CCA

Variables	VE	<i>F</i> -ratio	<i>P</i>
SO ₄ ^{2−}	0.247	4.485	0.0002*
Mg ²⁺	0.226	4.071	0.0004
Ca ²⁺	0.211	3.751	0.0008
<i>Q</i>	0.199	3.524	0.0022*
Oxí	0.157	2.723	0.0070
COND	0.141	2.414	0.0096
ST	0.136	2.332	0.0116
PO ₄ ^{3−}	0.121	2.049	0.0306
K ⁺	0.100	1.681	0.0830
Na ⁺	0.089	1.488	0.1328
NO ₃ [−]	0.088	1.474	0.1666
Cl	0.034	0.550	0.7530

DO = dissolved oxygen; TS = total solids; COND = conductivity; *Q* = discharge. VE = Explained variation in inertia units. Probability (*P*) and *F*-ratio refers to Monte Carlo test using 9999 permutations.

*Significant *P*-values (*P* < 0.01).

communication). The wide range of distribution of *Smicridea* sp. and *Americabaetis alphas* could explain the central position of these taxa in the ordination diagram of CA (C. Nieto, personal communication; P.A. Rueda Martín, personal communication; Wiggins, 1998). Also, these taxa are often abundant in streams of South America (Wiggins, 1998).

This study is the first in Argentina to test the seasonal variation of arthropod assemblages in monsoon climate streams. High discharge events cause the abundance and richness of arthropods to decline abruptly, but these effects are ameliorated by high-resilience taxa that rapidly recolonized streams. We suggest that future studies evaluating seasonal or temporal variability of benthic fauna may include other macroinvertebrate orders and environmental variables in order to identify “common denominators” of response to disturbance (Kelly and Harwell, 1990) and main seasonal changes associated with the monsoon climate.

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Appendix A

The list of taxa identified in Lules River Basin is shown in Table A1.

Table A1. List of taxa identified in Lules River Basin (abbreviations of taxa used in CA are also shown)

Coleoptera		Trichoptera	
Elmidae		Hydroptilidae	
<i>Austrelmis</i> sp. (adult)	<i>Ausa</i>	<i>Oxyethira</i> sp.	
<i>Austrelmis</i> sp. (larvae)	<i>Ausl</i>	<i>Hydroptila</i> sp.	
<i>Neaelmis</i> sp. (adult)		<i>Neotrichia</i> sp.	
<i>Neaelmis</i> sp. (larvae)		<i>Metrichia</i> sp.	<i>Met</i>
<i>Cylloepus</i> sp. (adult)		Leptoceridae	
<i>Macrelmis</i> sp. (larvae)		<i>Nectopsyche</i> sp.	
<i>Macrelmis</i> sp. (adult)		<i>Oecetis</i> sp.	
<i>Phanocerus</i> sp. (larvae)		Odontoceridae	
<i>Heterelmis</i> sp. (larvae)		<i>Marilia</i> sp.	
<i>Heterelmis</i> sp. (adult)		Helicopsychidae	
Dryopidae		<i>Helicopsyche</i> sp.	
<i>Helichus</i> sp. (adult)		Acari	
Ephemeroptera		Limnocharidae	
Baetidae		<i>Rhyncholimnochares expansiseta</i>	
<i>Baetodes</i> spp.	<i>Bae</i>	Rhynchohydracarinae	
<i>Camelobaetidius penai</i>	<i>Cam</i>	<i>Clathrosperchon punctatus</i>	
<i>Varipes</i> sp. (<i>minutus</i> + <i>singuil</i>)	<i>Var</i>	Hygrobatidae	
<i>Americabaetis alphas</i>	<i>Ame</i>	<i>Dodecabates dodecaporus</i>	
<i>Nanomis galera</i>	<i>Nan</i>	<i>Corticacarus</i> sp. <i>a</i>	
<i>Andesiops</i> sp.		<i>Corticacarus</i> sp. <i>c</i>	
Caenidae		<i>Corticacarus schwoerbeli</i>	
<i>Caenis</i> sp.		<i>Corticacarus smithi</i>	
Leptohyphidae		<i>Tetrahygrobatella bovala</i>	
<i>Leptohyphes eximius</i>	<i>Lep</i>	<i>Atractides sinuatipes</i>	
<i>Tricorythodes popayanicus</i>		<i>Atractides</i> sp. <i>a</i>	
<i>Haplohyphes baritu</i>		<i>Atractidella porophora</i>	
Leptophlebiidae		<i>Hygrobatella plebejus</i>	
<i>Thraulodes</i> sp.	<i>Thr</i>	<i>Hygrobatella multiacetabulata</i>	
Trichoptera		<i>Tetrahygrobatella argentinensis</i>	
Polycentropodidae		Aturidae	
<i>Polycentropus</i> sp.		<i>Axonopsella argentinensis</i>	
Philopotamidae		<i>Stygabliella tucumanensis</i>	
<i>Chimarra</i> sp.		Torrenicolidae	
Hydropsychidae		<i>Torrenticola columbiana</i>	<i>Tor</i>
<i>Smicridea</i> sp.	<i>Smi</i>	<i>Protolimnesia interstitialis</i>	
Hydrobiosidae		<i>Protolimnesia setifera</i>	
<i>Atopsyche</i> sp.		<i>Neomamersa mexicana</i>	
Glossosomatidae		<i>Diamphidaxona yungasa</i>	
<i>Mortoniella</i> sp.	<i>Mor</i>	<i>Meramecia</i> sp.	

References

- APHA, 1992. Standard Methods for the Examination of Water and Wastewater, 18th ed. American Public Health Association, New York.
- Archangelsky, M., 2001. Coleoptera. In: Fernández, H.R., Domínguez, E. (Eds.), Guide for Identification of South American Benthic Arthropods. EUdeT, University Press, Tucumán, Argentina, pp. 131–153 (in Spanish).
- Bêche, L.A., McElravy, E.P., Resh, V.H., 2006. Long-term seasonal variation in the biological traits of benthic-macroinvertebrates in two Mediterranean climate streams in California, U.S.A. *Freshwater Biol.* 51, 56–75.
- Boulton, A.J., Peterson, C.G., Grimm, N.B., Fisher, S.G., 1992. Stability of an aquatic macroinvertebrate community in a multiyear hydrologic disturbance regime. *Ecology* 73, 2192–2207.
- ter Braak, C.F.J., Prentice, I.C., 1988. A theory of gradient analysis. *Adv. Ecol. Res.* 18, 271–317.
- ter Braak, C.F.J., Šmilauer, P., 1998. CANOCO Reference Manual and User's Guide to Canoco for Windows. Software for Canonical Community Ordination (version 3.0). Microcomputer Power, Ithaca, NY.
- ter Braak, C.F.J., Verdonschot, P.F.M., 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquat. Sci.* 57, 255–289.
- Brooks, S.S., Boulton, A.J., 1991. Recolonization dynamics of benthic macroinvertebrates after artificial and natural disturbances in an Australian temporary stream. *Aust. J. Mar. Freshwater Res.* 42, 295–308.

- Brown, A.D., 2000. Development threats to biodiversity and opportunities for conservation in the mountain ranges of the upper Bermejo river basin, NW Argentina and SW Bolivia. *Ambio* 29, 445–449.
- Cummins, K.W., Merritt, R.W., Andrade, P.C.N., 2005. The use of invertebrate functional groups to characterize ecosystem attributes in selected streams and rivers in South Brazil. *Stud. Neotrop. Fauna Environ.* 40, 69–89.
- Di Sabatino, A., Martin, P., Gerecke, R., Cicolani, B., 2002. Hydrachnidia (water mites). In: Rundle, S.D., Robertson, A.L., Schmid-Araya, J.M. (Eds.), *Freshwater Meiofauna: Biology and Ecology*. Backhuys Publishers, Leiden, pp. 105–133.
- Dole-Oliver, M.J., Marmonier, P., Beffy, J.L., 1997. Response of invertebrates to lotic disturbance: is the hyporheic zone a patchy refugium? *Freshwater Biol.* 37, 257–276.
- Fernández, H.R., Molineri, C., 2006. Toward a sustainable experience in an intermountain valley from Northwestern of Argentina. *Ambio* 36, 262–266.
- Fernández, H.R., Palacios, A.N., 1989. The interstitial hyporheic fauna of two mountain rivers of Northwestern Argentina. *Riv. Idrobiol.* 28, 231–246.
- Flecker, A.S., Feifarek, B., 1994. Disturbance and the temporal variability of invertebrate assemblages in two Andean streams. *Freshwater Biol.* 31, 131–142.
- Fowler, R.T., 2004. The recovery of benthic invertebrate communities following dewatering in two braided rivers. *Hydrobiologia* 523, 17–28.
- Gauch, H.G., 1982. *Multivariate Analysis in Community Ecology*. Cambridge University Press, Cambridge.
- Golladay, S.W., Webster, J.R., Benfield, E.F., Swank, W.T., 1992. Changes in stream stability following forest clearing as indicated by storm nutrient budgets. *Arch. Hydrobiol.* 90 (Suppl.), 1–33.
- Gore, J.A., 1996. Discharge measurements and stream-flow analysis. In: Hauer, F.R., Lamberti, G.A. (Eds.), *Methods in Stream Ecology*. Academic Press, San Diego, pp. 53–74.
- Gray, L.J., Fisher, S.G., 1981. Postflood recolonization pathways of macroinvertebrates in a lowland Sonoran desert stream. *Am. Midl. Nat.* 106, 249–257.
- Grimm, N.B., Fisher, S.G., 1989. Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *J. North Am. Benthol. Soc.* 8, 293–307.
- Hendricks, A.C., Willis, L.D., Snyder, C., 1995. Impact of flooding on the densities of selected aquatic insects. *Hydrobiologia* 299, 241–247.
- Hill, M.O., Gauch, H.G., 1980. Detrended correspondence analysis, an improved ordination technique. *Vegetatio* 42, 47–58.
- Jacobsen, D., Encalada, A., 1998. The macroinvertebrate fauna of Ecuadorian high-land streams in the wet and dry season. *Arch. Hydrobiol.* 142, 53–70.
- Kelly, J.R., Harwell, M.A., 1990. Indicators of ecosystem recovery. *Environ. Manage.* 14, 527–545.
- Mainly, B.F.J., 1997. *Randomization, Bootstrap and Monte Carlo Methods in Biology*, second ed. Boca Raton, New York.
- Marchant, R., 1990. Robustness of classification and ordination techniques applied to macroinvertebrates communities from the La Trove River, Victoria. *Aust. J. Mar. Freshwater Resour.* 41, 493–504.
- McElravy, E.P., Lamberti, G.A., Resh, V.H., 1989. Year-to-year variation in the aquatic macroinvertebrate fauna of a Northern California stream. *J. North Am. Benthol. Soc.* 8, 51–63.
- Merritt, R.W., Cummins, K.W., 1996. *An Introduction to the Aquatic Insect of North America*, third ed. Kendall/Hunt, Dubuque.
- Mesa, L.M., 2006. Morphometric analysis of a subtropical Andean basin (Tucumán, Argentina). *Environ. Geol.* 50, 1235–1242.
- Minetti, J., Poblete, A.G., 2003. Climatic classification of Northwestern of Argentina. *Laboratorio climático sudamericano*. Fundación Caldenus, Universidad Nacional de Tucumán, Argentina (in Spanish).
- Mirande, V., 2001. The dynamic of phytoplankton of the Gastona river (Tucumán, Argentina) in relation to its water quality. Ph.D. Thesis, National University of Tucumán, Tucumán, Argentina (in Spanish).
- Negishi, J.N., Richardson, J.S., 2006. An experimental test of the effects of food resources and hydraulic refuge on patch colonization by stream macroinvertebrates during spates. *J. Anim. Ecol.* 75, 118–129.
- Nolte, U., de Oliveira, J.M., Stur, E., 1997. Season, discharge-driven patterns of mayfly assemblages in an intermittent neotropical stream. *Freshwater Biol.* 37, 333–343.
- Olsen, D.A., Townsend, C.R., 2005. Flood effects on invertebrates, sediments and particulate organic matter in the hyporheic zone of a gravel-bed stream. *Freshwater Biol.* 50, 839–853.
- Pierce, R.J., 1986. Foraging responses in stilts (*Himantopus* spp.): Aves) to changes in behaviour and abundance of their riverbed prey. *NZ J. Mar. Freshwater Res.* 20, 17–28.
- Resh, V.H., Brown, A.V., Covich, A.P., Gurtz, M.E., Li, H.W., Minshall, W.G., Reice, S.R., Sheldon, A.L., Bruce Wallace, J., Wissmar, R.C., 1988. The role of disturbance in stream ecology. *J. North Am. Benthol. Soc.* 7, 433–455.
- Robinson, C.T., Uehlinger, U., Hieber, M., 2001. Spatiotemporal variation in macroinvertebrate assemblages of glacial streams in the Swiss Alps. *Freshwater Biol.* 46, 1663–1672.
- del Rosario, R.B., Resh, V.H., 2000. Invertebrates in intermittent and perennial streams: is the hyporheic zone a refuge from drying? *J. North Am. Benthol. Soc.* 19, 680–696.
- Scrimgeour, G.J., Winterbourn, M.J., 1989. Effects of floods on epilithon and benthic macroinvertebrate populations in an unstable New Zealand river. *Hydrobiologia* 171, 33–44.
- Sedell, J.R., Reeves, G.H., Hauer, F.R., Stanford, J.A., Hawkins, C.P., 1990. Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. *Environ. Manage.* 14, 711–724.
- Smith, R.E.W., Pearson, R.G., 1987. The macroinvertebrate communities of temporary pools in an intermittent stream in tropical Queensland. *Hydrobiologia* 150, 45–61.
- Snook, D.L., Milner, A.M., 2002. Biological traits of macroinvertebrates and hydraulic conditions in a glacier-fed catchment (French Pyrénées). *Arch. Hydrobiol.* 153, 245–271.

- Wallace, J.B., 1990. Recovery of lotic macroinvertebrate communities from disturbance. *Environ. Manage.* 14, 605–620.
- Weigel, B.M., Wang, L., Rasmussen, P.W., Butcher, J.T., Stewart, P.M., Simon, T.P., Wiley, M.J., 2003. Relative influence of variables at multiple spatial scales on stream macroinvertebrates in the Northern Lakes and Forest ecoregion, U.S.A. *Freshwater Biol.* 48, 1440–1641.
- Wiggins, G.B., 1998. Larvae of the North American Caddisfly Genera (Trichoptera), second ed. University of Toronto Press, Toronto.
- Williams, D.D., Hynes, H.B.N., 1976. The ecology of temporary streams I. The fauna of two Canadian streams. *Internationale Rev. Hydrobiol.* 61, 761–787.
- Zar, J.H., 1996. *Biostatistical Analysis*, third ed. Prentice-Hall, Upper Saddle River, NJ.