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Crayfish as trophic agents: Effect of *Austropotamobius torrentium* on zoobenthos structure and function in small forest streams

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ABSTRACT

Key-words: *indigenous invertebrate, ecosystem engineer, headwaters, aquatic insects, functional feeding guilds*

Crayfish are among the largest and most threatened invertebrates in freshwater habitats. Due to their size, behaviour and feeding activity they may affect structure and function of aquatic ecosystems and their organisms. Despite their importance in many freshwaters and available information on their ecology for several species little is known about the European crayfish *Austropotamobius torrentium*. In order to evaluate the potential effects of indigenous crayfish presence on the structural and functional composition of the zoobenthic community, we measured population size and densities of three *A. torrentium* populations and compared macroinvertebrate assemblages and physicochemical parameters in three streams with and three without crayfish. The experimental setup considered crayfish effects at a large scale in defined reaches of pristine headwaters in association with the whole benthic fauna under natural conditions. Presence of *A. torrentium* significantly affected zoobenthic abundance, diversity and the relative proportions of functional feeding groups. In crayfish streams, especially Trichoptera and collector gatherers were more abundant and diverse, while sites without crayfish had significantly higher abundances and diversities of shredders and wood feeders. Our study provided strong evidence that the presence of the indigenous crayfish *A. torrentium* had important effects on the trophic cascades of headwater stream communities.

RÉSUMÉ

L'écrevisse comme agent trophique : effets d'*Austropotamobius torrentium* sur le zoobenthos et le fonctionnement de ruisseaux forestiers

Mots-clés : *invertébrés indigènes, espèce ingénieur, tête de bassin, insectes aquatiques, guilde alimentaire*

Les écrevisses sont parmi les invertébrés les plus menacés dans les habitats aquatiques. En raison de leur taille, de leur comportement et de leur nourriture, elles peuvent modifier la structure et le fonctionnement des écosystèmes aquatiques. Malgré leur importance dans beaucoup de milieux d'eau douce et les connaissances disponibles pour plusieurs espèces, peu de chose est connu sur l'écrevisse européenne *Austropotamobius torrentium*. Pour évaluer les effets potentiels de la présence de l'écrevisse indigène sur la structure spécifique et fonctionnelle de la communauté du zoobenthos, nous avons évalué les taille et densité de population de trois populations d'*A. torrentium* et comparé les assemblages de macroinvertébrés et les paramètres physico-chimiques dans trois ruisseaux avec écrevisses et trois sans écrevisses. Le dispositif expérimental considère les effets de l'écrevisse à une large échelle dans des tronçons de tête de bassin vierges de

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tout impact en association avec l'ensemble de la faune benthique dans ces conditions naturelles. La présence d'*A. torrentium* affecte significativement l'abondance du zoobenthos, sa diversité et les proportions relatives des groupes fonctionnels du réseau trophique. Dans les ruisseaux avec écrevisses, les trichoptères en particulier et les filtreurs sont plus abondants et variés, alors que dans les sites sans écrevisses l'abondance des brouteurs et décomposeurs de bois est significativement plus élevée. Notre étude montre clairement que la présence de l'écrevisse indigène a des effets importants sur les cascades trophiques des communautés de ruisseau de tête de bassin.

INTRODUCTION

Crayfish are among the largest invertebrates in freshwaters and may dominate the zoobenthic biomass (Haggerty *et al.*, 2002). Their presence is combined with wide impacts on aquatic ecosystems and trophic relationships therein, whereby crayfish are regarded as geomorphic agents and ecosystem engineers (Statzner *et al.*, 2000; 2003; Creed and Reed, 2004; Zhang *et al.*, 2004). Crayfish are recorded to affect filamentous algae (*e.g.* Creed, 1994; Charlebois and Lamberti, 1996), submersed macrophytes (*e.g.* Lodge and Lorman, 1987), the zoobenthos (*e.g.* Stenroth and Nyström, 2003), and even vertebrates like benthic fish (*e.g.* Guan and Wiles, 1997) and amphibians (*e.g.* Axelsson *et al.*, 1997). While crayfish are known to be omnivorous (*e.g.* Usio and Townsend, 2002), younger crayfish mainly feed on macroinvertebrates (*e.g.* Holdich *et al.*, 2006; Correia and Anastácio, 2007), directly affecting their abundance, biomass and taxa-richness (Nyström and Pérez, 1998; Usio, 2000; Stenroth and Nyström, 2003; McCarthy *et al.*, 2006; Gherardi and Acquistapace, 2007). Crayfish can even indirectly influence benthic communities by enhancing sediment transport and bioturbation (Statzner *et al.*, 2000; Statzner and Sagnes, 2008) or altering ecosystem structure, *e.g.* in transforming or providing food (Usio, 2000; Creed and Reed, 2004; Zhang *et al.*, 2004). These results suggest the crucial role of crayfish in aquatic systems, in particular the functional relationships of crayfish within the aquatic food webs. In this respect nothing is known about the stone crayfish *Austropotamobius torrentium* (Schrank) in association with the zoobenthos.

In Europe the remaining *A. torrentium* populations are threatened by several reasons, such as crayfish plague, alien crayfish species and habitat loss (Füreder and Souty-Grosset, 2005; Füreder *et al.*, 2006; Füreder, 2009). Although *A. torrentium* is one of the most endangered aquatic invertebrates in Europe, it is one of the least studied European freshwater crayfish (Souty-Grosset *et al.*, 2006; Füreder, 2009). As immediate management strategies are needed to protect and preserve *A. torrentium* in Europe, a detailed knowledge on its abiotic and biotic habitat requirements is necessary. While most habitat assessments of threatened crayfish species include abiotic requirements (*e.g.* Naura and Robinson, 1998; Streissl and Hödl, 2002a; Trouilhé *et al.*, 2007; Vlach *et al.*, 2009a, 2009b; but see Grandjean *et al.*, 2001; Brusconi *et al.*, 2008), only a few of the sparse studies dealing with *A. torrentium* considered assemblages of benthic invertebrates (Renz and Breithaupt, 2000; Auer, 2001; Weinländer and Füreder, 2010). No study, however, provided quantitative results on trophic relationships including this endangered crayfish species.

Austropotamobius torrentium has the narrowest distribution area of all native European crayfish (Holdich *et al.*, 2006) and its occurrence is mostly restricted to higher altitude streams with a relatively stable, stony bottom substrate (Machino and Füreder, 2005; Füreder *et al.*, 2006). Localities of *A. torrentium* are often isolated and difficult to find (Bohl, 1999), hence in Carinthia (Austria) still unexplored populations exist in isolated mountain streams (Weinländer and Füreder, 2008, 2010). In these small forested headwater streams the primary carbon source is allochthonous material derived from riparian vegetation and shredders, such as crayfish, play a major role in the breakdown of this coarse plant material (Vannote *et al.*, 1980). Especially crustaceans, but also insects can accelerate microbial processing of dead organic material (Covich *et al.*, 1999) and their leaf shredding enhances the food availability for other macroinvertebrates (Dieterich *et al.*, 1997).

Studies of crayfish effects usually examine impacts at small scales such as cages or channels (*e.g.* Usio, 2000; Stenroth and Nyström, 2003; Zhang *et al.*, 2004), but the role of crayfish in structuring the whole benthic fauna in larger stretches of streams is largely unknown. The aim of this study was to evaluate and quantify long-term effects of crayfish presence on macroinvertebrate assemblages in comparing a set of small forested streams with and without crayfish. We hypothesised that omnivorous *A. torrentium* should affect structure and function of benthic animal communities as an indirect effect of altered food resource availability.

MATERIAL AND METHODS

> *STUDY SITES*

The study was carried out in a mountainous and sparsely populated area in the Afritzer Nockberge (Gurktaler Alps) in Carinthia (Austria). The first to third order streams in this area historically harboured the two crayfish species *Astacus astacu*s (L.) and *A. torrentium*, but in the 1930s crayfish plague *Aphanomyces astaci* (Schikora) affected these populations, which were thought to be extinct since that time. In June 2006 a total of 21 streams were investigated at night from mouth to source in the communities of Fresach (WGS-84: 46° 43′ N, 13° 42′ E) and Ferndorf (46° 44′ N, 13° 38′ E) to determine crayfish presence or absence. While no existence of *A. astacus* could be confirmed any longer, seven streams were found having *A. torrentium*. Amongst them, the St. Jakober Bachl (S), the Weirerbach (W) and a tributary of the Tschernbachl in Glanz (G) were chosen for further investigations (Table I). For a later comparison of macroinvertebrate assemblages in streams with and without crayfish, three sites with similar habitat characteristics, but without *A. torrentium*, were selected: another tributary of the Tschernbachl (T), the orographic left (L) and right (R) upper course of the Koflerbach (Table I). Migration barriers like steep gradients, underground flow and technical obstructions prevented a natural recolonisation of these reaches by crayfish. All investigated stream sections had no visible anthropogenic impacts and were located within a linear distance of 2 km in mixed forests, mainly dominated by conifers. The riparian vegetation consisted of grey alder *Alnus incana* (L.), aquatic macrophytes were lacking, while bryophytes were present at all sites. All stream channels showed a high variability of width and depth, as well as heterogeneous flow patterns. In all streams, discharge, current velocity and water temperature were low with visible depths reaching the bottom during the investigations.

> *CRAYFISH*

After all streams were intensively searched for crayfish (night and day hand catch), detailed crayfish surveys were conducted in sites W, S and G by hand catch (turning stones) over a total of nine nights in July, August and October 2006. Experimental reaches were defined as 32 m long sections and were not blocked off to assure natural conditions. For each *A. torrentium*, sex was determined and carapace length (CL; from the tip of the rostrum to the posterior margin of the carapace) as well as total length were taken. Individuals were categorised into adults and juveniles according to Streissl and Hödl (2002b) and Huber and Schubart (2005), considering male *A. torrentium* with a CL smaller than 26 mm and females smaller than 31.5 mm as immature, while crayfish under 10 mm CL were categorised as young of the year (YOY). After length measurements, wet mass (g) was measured after dubbing water off the crayfish. Each specimen was marked permanently (individual perforation of the uropods or telson) and released within its home range. In all streams, population size was determined for a 32 m section by applying the Peterson-method, modified after Bailey (1952):

$$N = (M \times (C + 1))/R + 1$$

Where N is the estimate of the population size, M the number of individuals captured in the first catch, C the total number of individuals captured in the second catch and R the number

Table I
Site description and physico-chemistry of the investigated streams measured in October 2006. W = Weirerbach, G = Tschernbachl (Glanz), S = St. Jakober Bachl, R = right upper course of the Koflerbach, T = Tschernbachl (Gschriet), L = left upper course of the Koflerbach, n.m. = not measured.

Tableau I
Description des sites et paramètres abiotiques des ruisseaux étudiés en octobre 2006. W = Weirerbach, G = Tschernbachl (Glanz), S = St. Jakober Bachl, R = tributaire droit du Koflerbach, T = Tschernbachl (Gschriet), L = tributaire gauche du Koflerbach, n.m. = non mesuré.

		W	G	S	R	T	L
		Crayfish			No crayfish		
Catchment		Drave	Lieser	Drave	Lieser	Lieser	Lieser
Latitude	WGS-84	46° 44′ 14.56″	46° 45′ 14.17″	46° 44′ 30.29″	46° 46′ 16.72″	46° 45′ 17.83″	46° 46′ 14.63″
Longitude	WGS-84	13° 39′ 40.66″	13° 38′ 49.25″	13° 38′ 17.90″	13° 39′ 58.63″	13° 39′ 35.83″	13° 39′ 58.24′
Altitude	(m a.s.l.)	760	810	720	982	939	995
Stream order		2	1	2	2	2	2
Stream length	(km)	7.8	1.9	4.9	3.3	2.1	2.8
Mean width	(m)	1.87	0.94	1.34	1.03	0.9	0.69
Mean depth	(cm)	13.9	8.4	9.6	9.5	10.5	6.8
Mean velocity	(cm·s^{-1})	14.1	14.3	16.7	15	12.5	17.5
Water temperature	(°C)	10.4	10.4	12	8.4	10.9	8.7
Mud ($<$ 0.063 mm)	(%)	10	-	10	-	10	-
Sand (0.063–2 mm)	(%)	5	10	5	10	5	10
Gravel ($>$ 0.2–2 cm)	(%)	15	30	5	15	5	10
Stones ($>$ 2 cm)	(%)	55	55	70	55	70	70
Woody debris	(%)	15	5	10	20	10	10
Cond.	(µS)	150	171	334	80.90	257	51.50
pH		7.58	7.42	7.78	7.73	8.03	7.22
O_2	(mg·L^{-1})	9.2	9.3	9.3	n.m.	n.m.	n.m.
O_2	(%)	73	74	74	n.m.	n.m.	n.m.
NO_3^-	(µg·L^{-1})	104	158	1943	357	781	497
SO_4^-	(mg·L^{-1})	4.68	5.15	14.31	4.84	5.70	5.35
Cl	(mg·L^{-1})	13.61	32.2	23.13	0.61	24.47	0.74
NH_4^+	(µg·L^{-1})	1	1	3	1	6	1
Na	(mg·L^{-1})	7.95	14.25	10.24	1.92	14.56	1.71
K	(mg·L^{-1})	1.65	1.47	12.72	1.34	6.09	1.27
Mg	(mg·L^{-1})	5.43	5.32	12.33	2.21	5.82	1.75
Ca	(mg·L^{-1})	12.68	7.2	36.16	10.36	23.79	5.05
TP	(µg·L^{-1})	17.4	8.6	14.6	11.70	136.60	14.60
DRP	(µg·L^{-1})	7.1	3.7	12.3	1.10	112.60	2
TDN	(mg·L^{-1})	0.32	0.32	2.34	0.41	0.96	0.58
DOC	(mg·L^{-1})	7.06	5.69	7.93	1.75	3.50	2.63

of marked individuals from the second catch (Krebs, 1989). After the population size was known for the 32 m stream sections, crayfish densities (ind.·m^{-2}) were calculated.

> BENTHIC INVERTEBRATES

To compare macroinvertebrate assemblages in streams with and without crayfish (Table I) a total of 60 bottom samples (10 per 32 m stream lengths, with and without crayfish) were taken in July (n = 30) and September (n = 30) 2006 with a Surber sampler (mesh size 100 µm, 20 × 20 cm sampled area). The sampled substrate consisted of stones (diameter $<$ 20 cm), or leaf detritus from shallow areas ($\leqslant$ 10 cm). *In situ*, samples were preserved in 70% ethanol. In the laboratory samples were divided into $>$ 1000 µm, $>$ 500 µm and $>$ 100 µm fractions and benthic animals were sorted into major taxonomic groups. Larvae of Ephemeroptera, plecoptera and trichoptera (EPT) were identified mostly to species, some to genus level, diptera larvae to families, while other taxa were grouped into orders. Following Moog (2002) the saprobic index was calculated for all taxa and for 77 invertebrate taxa a categorisation into the following functional feeding groups and their nutriments was possible: shredders

Table II
Estimation of population size and density for a 32 m section in each stream with length measurements of A. torrentium*. N = estimate of the population size, M = number of individuals captured in the first catch, C = total number of individuals captured in the second catch, R = number of marked individuals from the second catch.*

Tableau II
Estimation de la taille des populations et de leur densité pour un tronçon de 32 m dans chaque ruisseau avec mensurations d'*A. torrentium*. *N* = estimation de la population, *M* = nombre d'individus capturés au premier passage, *C* = nombre total d'individus capturés au second passage, *R* = nombre d'individus marqués capturés au second passage.

						Carapace length (mm)				
	M	*C*	*R*	*N*	ind.·m^{-2}	*n*	Mean	± SD	Min	Max
Weirerbach (W)	56	40	1	1148	19.2	158	26.3	6.7	5.6	44.6
Tschernbachl (G)	17	11	3	51	1.7	31	30.5	7.4	18.5	43.9
St. Jakober Bachl (S)	48	52	2	848	19.8	156	24.1	8.2	11	41.6

(fallen leaves, plant tissue, CPOM), grazers (epilithic algal tissues, biofilm, partially POM, tissues of living plants), collectors (active or passive filtration of suspended FPOM, CPOM and micro prey), detritus feeders (sedimented FPOM), wood feeders (woody debris) and predators (animal prey).

> *STATISTICAL ANALYSIS*

Samples taken in July and September were combined for the analyses to build larger data sets. Abundance, number of taxa, Shannon–Wiener diversity index (binary log) and Evenness were calculated in EcologiXcel 1.2 (MS Excel Add-In: Spreadsheet Functions for Ecology) for the total zoobenthos, EPT taxa and functional feeding groups, respectively. For the taxa with a good indicator potential and a high taxonomic resolution (EPT) a two-way cluster analysis with Bray Curtis linkage distance was performed in PC-ORD 5.01 to show similarities between and within sites with and without crayfish on species level. Canonical correspondence analysis (CCA) was calculated in Canoco 4.5 to include physicochemical parameters (Table I) and the abundances of *A. torrentium* and 77 taxa with their functional feeding groups to compare the trophic level in streams with and without crayfish. To clarify the differences in the abundances, number of taxa and diversities of the investigated taxa and feeding types between crayfish and non crayfish sites the overall statistical significance was tested with MANOVAs (Wilks' lamda test) in PASW Statistics 18. When MANOVAs were statistically significant, individual one-way ANOVAs and Tukey's *post hoc* tests were performed with SigmaPlot 9.0. For both analyses of variance the statistical level of significance was set at $P < 0.05$. Some values of physicochemical parameters (Table I) were excluded from the CCA either due to incompleteness (oxygen) or due to a stepwise detection of variables with an inflation factor above 20 (conductivity, NO_3^-, Na^+ and K^+). To counteract the disproportion of abundant and rare taxa resulting from the high taxonomic resolution, taxa abundance was square-root transformed for the CCA, MANOVAs and one-way ANOVAs.

RESULTS

> *POPULATION SIZE AND DENSITY OF* A. TORRENTIUM

In the Weirerbach (W) crayfish were found in the total stream length of 7.82 km, while in the other streams the distribution of *A. torrentium* was limited to the headwaters, where only 0.35 km were occupied in the Tschernbachl (G) and 0.75 km in the St. Jakober Bachl (S). A total of 345 *A. torrentium* were caught in all stream sections (Table II), which resulted in population size estimates of 1148 individuals (39.1% adults, 60.9% juveniles with 5.3% YOY)

Table III
Mean abundance (ind.·m^{-2} ± SE), number of taxa, Shannon–Wiener diversity, evenness and saprobic index of the sampled aquatic macroinvertebrates and terrestrial bycatch in the studied streams (10 samples per site). W = Weirerbach, G = Tschernbachl, S = St. Jakober Bachl, R = right upper course of the Koflerbach, T = Tschernbachl, L = left upper course of the Koflerbach.

Tableau III
Abondance moyenne (ind.·m^{-2} ± SE) du zoobenthos échantillonné, nombre de taxons, indice de diversité de Shannon-Wiener, équitabilité et indice saprobie des sites étudiés (10 échantillons par site). W = Weirerbach, G = Tschernbachl, S = St. Jakober Bachl, R = tributaire droit du Koflerbach, T = Tschernbachl, L = tributaire gauche du Koflerbach.

	W	G	S	R	T	L
	Crayfish			No crayfish		
	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
“Vermes”						
Turbellaria	-	6.3±4.2	-	62.5±28.2	215.6±72.4	28.1±24.8
Oligochaeta	140.6±124.2	28.1±28.1	12.5±12.5	18.8±8.3	2903.1±1083.7	15.6±9.6
Mollusca						
Bivalvia	-	-	28.1±24.8	-	15.6±9.6	-
Arachnida						
Araneae	-	6.3±6.3	3.1±3.1	-	-	6.3±4.2
Acari	496.9±301.1	153.1±119.8	15.6±8.4	-	200.3±200.3	165.6±141.9
Opiliones	-	3.1±3.1	-	-	9.4±9.4	3.1±3.1
Crustacea						
Isopoda	-	3.1±3.1	-	-	3.1±3.1	-
Gammaridae	2965.6±648.8	143.8±65.7	3.1±3.1	596.9±411.2	12 225.2±5362.7	1209.4±398.1
Cyclopoidea	-	-	-	-	65.6±41.3	-
“Myriapoda”						
Diplopoda	-	-	-	-	3.1±3.1	-
Insecta						
Ephemeroptera	4425.1±1395.3	3406.3±1049.8	687.5±218.7	1300.3±274.4	1181.3±279.7	2018.8±647.2
Trichoptera	887.5±276.1	865.6±286.5	825±158.1	400.1±94.1	346.9±92.4	178.1±85.3
Plecoptera	978.1±210.4	3290.6±1161.1	2425.1±557.1	1675.1±421.6	2165.6±700.8	965.6±253.9
Diptera larvae	6887.5±2806.8	11 071.9±3987.6	6403.1±1826.7	6471.9±1851.1	6234.4±1822.1	1775.2±315.2
Nematocera (adult)	-	-	-	-	3.1±3.1	3.1±3.1
Coleoptera	437.5±163.8	34.4±19.5	75.2±32.1	34.4±17.1	290.6±193.4	81.3±34.9
Coleoptera larvae	540.6±113.3	28.1±13.5	25±13.8	28.1±9.8	275.1±192.7	106.3±28.4
Odonata	6.3±4.2	15.6±7.2	3.1±3.1	-	200±200	-
Heteroptera	6.3±6.3	15.6±7.2	-	-	200±200	-
Collembola	-	3.1±3.1	28.1±28.1	-	25±17.3	-
Total	17 771.9±2957.1	19 075.2±5561.8	10 534.4±2091.6	10 587.5±2123.1	26 562.5±7774.1	6556.3±1219.8
Number of taxa	66	76	56	55	64	55
Shannon–Wiener	2.69	2.68	2.45	2.47	2.37	2.78
Evenness	0.59	0.58	0.55	0.55	0.52	0.65
Saprobic index	1.43	1.46	1.59	1.12	1.47	1.45

in site W, 51 in G (58.1% adults and 41.9% juveniles, no YOY) and 848 in S (31.6% adults, 68.4% juveniles, including 5.8% YOY). Population densities of *A. torrentium* ranged from high in the St. Jakober Bachl (19.8 ind.·m^{-2}) and Weirerbach (19.2 ind.·m^{-2}) to comparatively low (1.7 ind.·m^{-2}) in the Tschernbachl (Table II). The stream sections with high *A. torrentium* densities in sites S and W showed a well balanced sex ratio of 1:1.12 (n = 156; male:female) in the St. Jakober Bachl and 1:0.93 (n = 158; m:f) in the Weirerbach, but was less balanced in the Tschernbachl (G) with 1:0.63 (n = 31; m:f). Crayfish total length and wet mass varied from 18 to 91 mm and 0.2 to 33.9 g in males and 17 to 85 mm and 0.1 to 22.3 g in females.

> *BENTHIC MACROINVERTEBRATES IN STREAMS WITH AND WITHOUT CRAYFISH*

A total of 105 different macroinvertebrate taxa were found in all sites, indicating a good water quality in all streams based on low saprobic indices, ranging from 1.12 in site R to 1.59 in site S (Table III). The zoobenthos was dominated by Diptera (mainly Chironomidae), followed

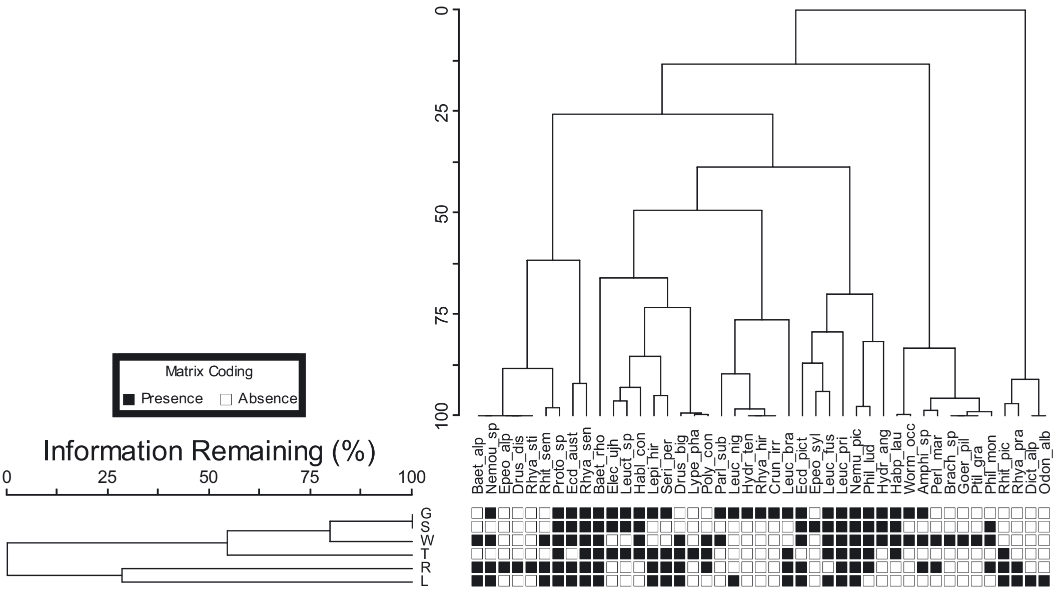

Figure 1

Dendrogram from two-way cluster analysis showing the relative similarity of the investigated streams and 43 Ephemeroptera, Plecoptera and Trichoptera taxa. Linkage method: centroid, distance measure: Sorensen (Bray Curtis). Crayfish streams: W = Weirerbach, G = Tschernbachl (Glanz), S = St. Jakober Bachl; no crayfish: R = right upper course of the Koflerbach, T = Tschernbachl (Gschriet), L = left upper course of the Koflerbach.

Figure 1

Diagramme de l'analyse hiérarchique montrant les similarités relatives des ruisseaux étudiés et les 43 taxons d'éphéméroptères, plécoptères et trichoptères. Méthode : centroïdes, mesure de distance : Sorensen (Bray Curtis). Ruisseau avec écrevisses : W = Weirerbach, G = Tschernbachl (Glanz), S = St. Jakober Bachl ; sans écrevisses : R = tributaire droit du Koflerbach, T = Tschernbachl, L = tributaire gauche du Koflerbach.

by Ephemeroptera, Plecoptera and Trichoptera (EPT), except for site T, where Gammaridae were most abundant and Oligochaeta were frequent (Table III). The highest number of taxa was found in site G with *A. torrentium*, while highest diversity index and evenness was found in site L without crayfish (Table III).

Cluster analysis classified a high similarity for localities with crayfish compared to sites without crayfish. Species composition and abundance of 43 EPT taxa (Table IV) clearly discriminated streams with and without crayfish, shown in the linkage distances on the left tree diagram of the two-way cluster dendrogram (Figure 1). Crayfish streams (G, S, W) had a similarity of about 80% based on EPT, whereas in streams without crayfish (R, L, T) similarity was lower. Two streams without crayfish (R, L) were clearly separated from all other sites and had a low similarity of about 25%, while site T had a similarity of over 50% with the crayfish streams. This pattern is supported by a relatively high first level of fusion (about 60%) in the right dendrogram, also confirming this strong affinity of certain EPT taxa based on their abundances. Their presence or absence, which is shown in the matrix below, demonstrates the underlying consistency of the individual taxa in their species composition (Figure 1). Most common taxa, occurring in all streams, were *Baetis rhodani*, *Nemurella pictetii*, *Protonemura* sp., *Rhyacophila* (*sensu stricto*) sp. and larvae of the *Leuctra prima-hippopus-inermis* group (Figure 1, Table IV). Rare and least consistent taxa were *Epeorus alpicola*, *Drusus discolor* and *Rhyacophila stigmatica* (only in site R), *Epeorus sylvicola* (site S), *Lype phaeopa* (site T), *Hydropsyche tenuis*, *Rhyacophila hirticornis* and *Crunoecia irrorata* (site G), *Brachyptera* sp., *Goera pilosa* and *Ptilocolepus granulatus* (site W), as well as *Dictyogenus alpinum/fontium* and *Odontocerum albicorne* (site L).

Table IV
Ephemeroptera, Plecoptera and Trichoptera identified in this study with their abbreviations used in cluster analysis.

Tableau IV
Éphéméroptères, plécoptères et trichoptères identifiés dans l'étude et leurs abréviations dans l'analyse hiérarchique.

	Taxa
	Ephemeroptera
Baet_alp	*Baetis alpinus* Pictet, 1843–1845
Baet_rho	*Baetis rhodani* Pictet, 1843–1845
Ecd_aust	*Ecdyonurus austriacus* Kimmins, 1958
Ecd_pict	*Ecdyonurus picteti* (Meyer-Dür, 1864)
Elec_ujh	*Electrogena ujhelyii* (Sowa, 1981)
Epeo_alp	*Epeorus alpicola* (Eaton, 1871)
Epeo_syl	*Epeorus sylvicola* (Pictet, 1865)
Habl_con	*Habroleptoides confusa* Sartori & Jakob, 1986
Habp_lau	*Habrophlebia lauta* Eaton, 1884
Parl_sub	*Paraleptophlebia submarginata* (Stephens, 1835)
Rhit_pic	*Rhithrogena c.f. picteti* Sowa,1971
Rhit_sem	*Rhithrogena semicolorata* (Curtis, 1834)
	Plecoptera
Amphi_sp	*Amphinemura* sp. Ris, 1902
Brach_sp	*Brachyptera* sp. Newport, 1849
Dict_alp	*Dictyogenus alpinum/fontium* (Pictet, 1841)/(RIS, 1896)
Leuc_bra	*Leuctra braueri* Kempny, 1898
Leuc_fus	*Leuctra fusca*-group (Linnaeus, 1758)
Leuc_nig	*Leuctra nigra* (Olivier, 1811)
Leuc_pri	*Leuctra prima-hippopus-inermis*-group Kempny, 1898
Leuct_sp	*Leuctra* sp. Stephens, 1836
Nemou_sp	*Nemoura* sp. Latreille, 1796
Nemu_pic	*Nemurella pictetii* Klapálek, 1900
Perl_mar	*Perla marginata* (Panzer, 1799)
Proto_sp	*Protonemura* sp. Kempny, 1898
	Trichoptera
Crun_irr	*Crunoecia irrorata* (Curtis, 1834)
Drus_big	*Drusus biguttatus* (Pictet, 1834)
Drus_dis	*Drusus discolor* (Rambur, 1842)
Goer_pil	*Goera pilosa* (Fabricius, 1775)
Hydr_ang	*Hydropsyche angustipennis* (Curtis, 1834)
Hydr_ten	*Hydropsyche tenuis* Navas, 1932
Lepi_hir	*Lepidostoma hirtum* (Fabricius, 1775)
Lype_pha	*Lype phaeopa* (Stephens, 1936)
Odon_alb	*Odontocerum albicorne* (Scopoli, 1763)
Phil_lud	*Philopotamus ludificatus* Mc Lachlan, 1865
Phil_mon	*Philopotamus montanus* (Donovan, 1813)
Poly_con	*Plectrocnemia* c.f. *conspersa* (Curtis, 1803)
Ptil_gra	*Ptilocolepus granulatus* (Pictet, 1834)
Rhya_hir	*Rhyacophila hirticornis* Mc Lachlan, 1879
Rhya_pra	*Rhyacophila praemorsa/polonica* Mc Lachlan, 1879
Rhya_sen	*Rhyacophila* (*sensu stricto*) sp. Pictet, 1834
Rhya_sti	*Rhyacophila stigmatica* Kolenati, 1859
Seri_per	*Sericostoma personatum/flavicorne* (Kirby & Spence, 1826)
Worm_occ	*Wormaldia occipitalis* (Pictet, 1834)

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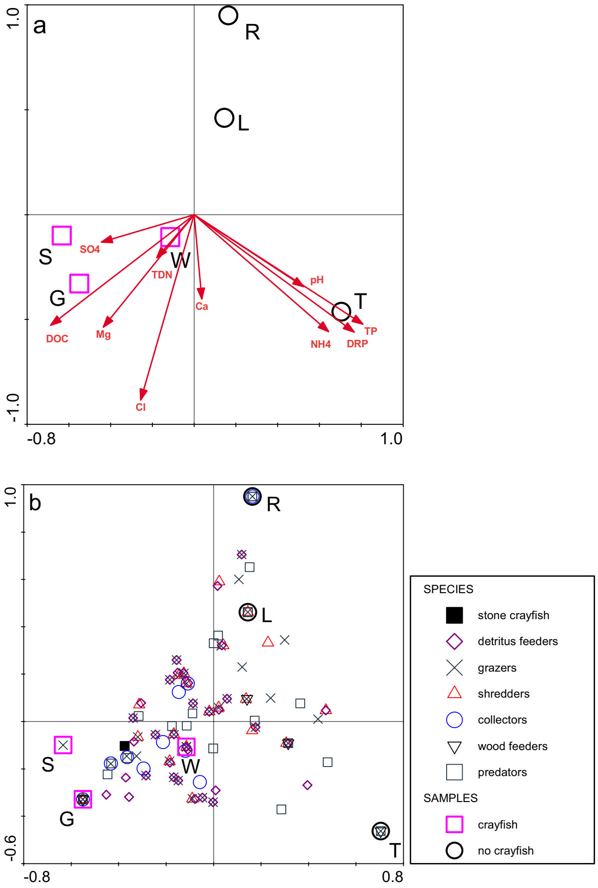

Figure 2

Correlation plots from the CCA with (a) sample sites and environmental variables and (b) sample sites and species data, including A. torrentium *and 77 invertebrates with their functional feeding group. W = Weirerbach, G = Tschernbachl (Glanz), S = St. Jakober Bachl, R = right upper course of the Koflerbach, T = Tschernbachl (Gschriet), L = left upper course of the Koflerbach.*

Figure 2

Graphes d'analyse canonique des correspondances avec (a) sites échantillonnés et variables environnementales et (b) sites échantillonnés et données spécifiques incluant *A. torrentium* et 77 invertébrés et leur groupe trophique. W = Weirerbach, G = Tschernbachl (Glanz), S = St. Jakober Bachl ; sans écrevisses : R = tributaire droit du Koflerbach, T = Tschernbachl, L = tributaire gauche du Koflerbach.

The CCA based on sample sites, functional feeding groups and measured abiotic variables supported the results from the cluster analysis (Figure 2). Total inertia reached 0.713, where the first (35.3%) and second axis (25.1%) explained 60.4% of the cumulative variance in the species data and environmental variables. Total phosphorous had the strongest correlation to axis 1, while chloride to axis 2 (Figure 2a). A high correlation was found between ammonium and dissolved (r^2 = 0.95), as well as total (r^2 = 0.96) phosphorous and pH (r^2 = 0.84), which were all associated to site T (Figure 2a). Crayfish sites were positioned close to dissolved organic carbon, magnesium and chloride, while sites without crayfish were negatively correlated to these variables. However, physicochemical measurements (Table I) showed no overall significant differences between streams with and without *A. torrentium* (MANOVA: F = 0.664; df = 4, 1; P = 0.713). The pattern of site and species arrangements (Figure 2b) clearly distinguished streams with and without crayfish. Whereas crayfish sites had higher relative abundances and frequencies of collecting and detritus feeding species, shredders were more associated to sites without crayfish. The stone crayfish is included in the analysis,

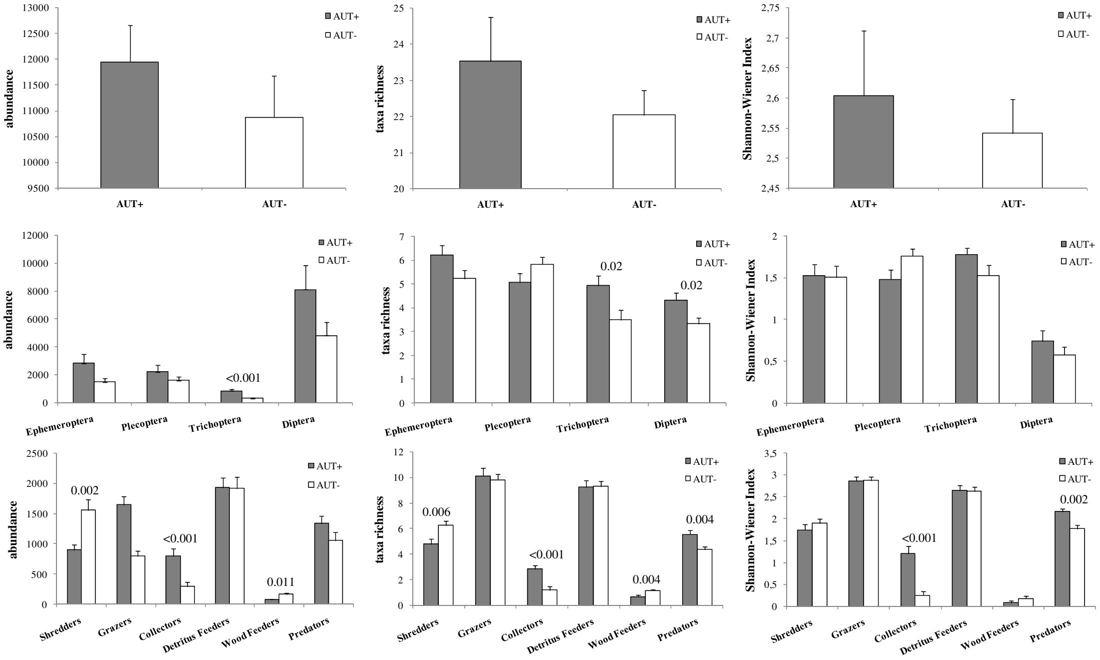

Figure 3
Mean abundance (ind.$\cdot$m^{-2}), taxa richness and Shannon–Wiener index with standard errors (± SE) and significant P-values of the total zoobenthos (above), Ephemeroptera, Plecoptera, Trichoptera and Diptera larvae (middle) and trophic guilds (below). AUT+ = A. torrentium *present, AUT- =* A. torrentium *absent (30 zoobenthos samples in each stream type).*

Figure 3
Abondance moyenne (ind.$\cdot$m^{-2}), richesse en taxons, indice de Shannon-Wiener avec erreurs standard (± SE) et valeur seuil de P significative pour le zoobenthos total (partie supérieure), larves d'éphéméroptères, plécoptères, trichoptères et diptères (au milieu) et guildes trophiques (en bas). AUT+ = *A. torrentium* présente, AUT- = *A. torrentium* absente (30 échantillons de zoobenthos dans chaque site).

therefore functional feeding types positioned at or in proximity of its symbol, indicating closest association to collectors and detritus feeders.

Overall significant differences (MANOVA) between sites with and without crayfish were also found in the abundances ($F = 7.222$; df = 11, 48; $P < 0.001$), taxa richness ($F = 8.934$; df = 11, 48; $P < 0.001$) and Shannon–Wiener diversity indices ($F = 8.865$; df = 11, 48; $P < 0.001$) of grouped invertebrate taxa and functional feeding groups. Individual one-way ANOVAs identified a significant higher abundance, taxa richness and diversity of collectors in streams with *A. torrentium*, while shredders and wood feeders were significantly less abundant (Figure 3, Table V). Crayfish sites had a significantly higher taxa richness of Diptera, as well as abundances and taxa richness of Trichoptera (Figure 3, Table V). Also the taxa richness and Shannon–Wiener diversity index of predators were significantly higher in sites with *A. torrentium* (Figure 3, Table V). There was no significant difference in abundance, taxa richness and Shannon–Wiener diversity of the total zoobenthos (Figure 3, Table V).

Table V
Summary of one-way ANOVAs with abundance, taxa richness and Shannon–Wiener diversity index of the total zoobenthos, Ephemeroptera, Plecoptera, Trichoptera, Diptera larvae and the trophic guilds in crayfish streams against sites without crayfish. Significant values in bold.

Tableau V
Résultats de l'analyse de variance simple sur les abondances, la richesse taxonomique et l'indice de diversité de Shannon-Wiener du zoobenthos total, des éphéméroptères, des plécoptères, des trichoptères, des larves de diptères et des guildes trophiques dans les ruisseaux à écrevisses et les sites sans écrevisses. Les valeurs significatives sont en gras.

Source		d.f.	MS	F	P	d.f.	MS	F	P	d.f.	MS	F	P
		Abundance				Taxa richness				Diversity			
Total	Crayfish effect	1	173 825.687	0.991	0.324	1	33.75	1.135	0.291	1	0.0245	0.11	0.741
	Residual	58				58				58			
Ephemeroptera	Crayfish effect	1	269 172.526	3.817	0.056	1	14.017	2.923	0.093	1	0.0092	0.0164	0.899
	Residual	58				58				58			
Plecoptera	Crayfish effect	1	59 377.604	1.357	0.249	1	8.817	2.458	0.122	1	1.185	3.631	0.062
	Residual	58				58				58			
Trichoptera	Crayfish effect	1	45 547.038	13.9	< **0.001**	1	30.817	5.704	**0.02**	1	0.938	2.986	0.089
	Residual	58				58				58			
Diptera	Crayfish effect	1	1 627 318.359	2.836	0.098	1	15	5.749	**0.02**	1	0.413	1.056	0.308
	Residual	58				58				58			
Shredders	Crayfish effect	1	64 487.538	10.71	**0.002**	1	32.267	8.044	**0.006**	1	0.332	0.773	0.383
	Residual	58				58				58			
Grazers	Crayfish effect	1	742.249	0.169	0.683	1	1.35	0.157	0.694	1	0.00453	0.0178	0.894
	Residual	58				58				58			
Collectors	Crayfish effect	1	38 703.356	18.148	< **0.001**	1	45.067	28.026	< **0.001**	1	12.863	34.149	< **0.001**
	Residual	58				58				58			
Detritus feeders	Crayfish effect	1	27.225	0.00275	0.958	1	0.0667	0.00868	0.926	1	0.00404	0.0115	0.915
	Residual	58				58				58			
Wood feeders	Crayfish effect	1	1270.005	6.925	**0.011**	1	3.267	9.257	**0.004**	1	0.13	1.342	0.251
	Residual	58				58				58			
Predators	Crayfish effect	1	12 105.874	2.439	0.124	1	21.6	8.802	**0.004**	1	2.237	10.266	**0.002**
	Residual	58				58				58			

DISCUSSION

> BENTHIC MACROINVERTEBRATES IN STREAMS WITH AND WITHOUT CRAYFISH

Our field experiment in natural habitat conditions of small headwater streams with and without crayfish revealed quite contrasting patterns regarding the structure and function of benthic invertebrate composition. While non-significant or minor differences in conventional parameters, like total abundances, taxa number and diversity, were detected, strong evidence for the potential effect of crayfish on the trophic interactions exists. Distribution, population size and density of *A. torrentium* also showed differences in the investigated crayfish streams. Especially in the Weirerbach (W) *A. torrentium* was widespread, occurring in the whole stream from mouth to source in different substrate types. This is in contrast to the St. Jakober Bachl (S) and Tschernbachl (G), where crayfish occurrence was limited to relatively short stretches in the headwaters with stony substrate. These conditions are typical for this species (Renz and Breithaupt, 2000; Füreder *et al.*, 2006; Holdich *et al.*, 2006). The crayfish populations in S and G were fragmented and confined to distinct stretches due to natural migration barriers (steep gradients, subterranean stream sections), as well as artificial obstructions (piping under streets), preventing a natural spreading of the species today. This situation was found to be ideal for the design of the natural field experiment. Apart from the higher crayfish densities in two streams (W and S), environmental conditions were well comparable to other stone crayfish locations (Renz and Breithaupt, 2000; Auer, 2001; Huber and Schubart, 2005; Füreder *et al.*, 2006; Holdich *et al.*, 2006). The two streams (W and S) with *A. torrentium* densities of almost 20 ind.$\cdot$m^{-2} showed a functioning reproduction with juveniles dominating and the presence of YOY. In site G, however, crayfish reached a low density of about 2 ind.$\cdot$m^{-2}. The population was dominated by adults, the percentage of juveniles was normal but YOY were lacking. Notwithstanding the differing crayfish densities, the effect on the zoobenthos was observed in all crayfish sites.

The benthic community was found to be typically composed of the dominating Diptera (mainly Chironomidae) and various taxa within the orders EPT, as also recorded from other studies where the white-clawed crayfish *Austropotamobius pallipes* (Lereboullet) was the indigenous species (Grandjean *et al.*, 2001, 2003; Reynolds and O'Keeffe, 2005). Some studies showed that amphipods dominated the fauna in streams with *A. torrentium* (Renz and Breithaupt, 2000; Auer, 2001) and *A. pallipes* (Trouilhé *et al.*, 2003). In our study *Gammarus* sp. was only common in one of the streams with crayfish (W), whereas this shredding species was more frequent in streams without crayfish. Especially in T, *Gammarus* sp. dominated the total zoobenthos. In the latter stream oligochaetes were also common. On the one hand we assume that crayfish takes over the role as a shredder and on the other hand as an omnivorous species feeds on oligochaetes.

Crayfish presence did not affect abundance, number of taxa and diversity of the total zoobenthos, which is supported by a study of Bondar *et al.* (2005), while in other studies the opposite was recorded (Creed and Reed, 2004; Usio and Townsend, 2004; Zhang *et al.*, 2004; Gherardi and Acquistapace, 2007). Most of these studies were carried out in more or less closed conditions (enclosures), where the availability, type and selection of potential food were limited and therefore effects on associated invertebrates stronger. In the natural setting of our field experiment interactions and effects might have remained more complex.

Direct comparison of the two stream types in cluster analysis otherwise indicated a high similarity of crayfish streams and their associated taxa of Ephemeroptera, Plecoptera and Trichoptera. Crayfish streams had significantly higher abundances and diversities of Trichoptera and many species from this order, like *Crunoecia irrorata*, *Goera pilosa*, *Hydropsyche tenuis*, *Ptilocolepus granulatus* and *Rhyacophila hirticornis*, were exclusively found with crayfish presence. Also the CCA confirmed a high similarity of crayfish streams in respect of the trophic guilds, where especially the abundance and diversity of collectors, detritus feeders and shredders showed interesting patterns in the benthic fauna.

We attribute these dissimilarities primarily to the presence and absence of crayfish. Other possible causes, like differences in the environmental parameters may play a minor role. Our CCA results derive from a restricted area with a limited environmental variation, as all benthic samples were taken from the same habitat and substrate. As a consequence, no gradient based on environmental variables was expected *a priori* and also stream morphology and physicochemical parameters showed no significant differences. Also the saprobic indices confirmed a high water quality in all sites and therefore support low long-term variations in nutrient levels. Some of the variations in physico-chemistry might be related to geology, individual surroundings, temporal enrichment and also to crayfish presence. As leaf shredding insects were found to increase DOC in headwaters (Meyer and O'Hop, 1983), higher DOC concentrations in streams with *A. torrentium* might be a direct result from the shredding activity of crayfish themselves (Usio, 2000; Creed and Reed, 2004; Zhang *et al.*, 2004). Other than environmental parameters crayfish presence/absence rather provide strong evidence for structuring the functional organisation of the community. Collectors and detritivores were mainly related to sites with crayfish and shredders to streams lacking crayfish. Sites with *A. torrentium* had significantly higher abundances and diversities of collectors and predators, while shredders and wood feeders were lower abundant and diverse.

It is known that crayfish predation can directly reduce several invertebrate taxa (Nyström and Pérez, 1998; Usio, 2000; Stenroth and Nyström, 2003; McCarthy *et al.*, 2006; Nyström *et al.*, 2006; Gherardi and Acquistapace, 2007), but also their habitat alteration, bioturbation and sediment transport can have indirect effects on the zoobenthos distribution in freshwaters (Statzner *et al.*, 2000, 2003; Usio and Townsend, 2004; Statzner and Sagnes, 2008). In our study all investigated streams were near the source in forested areas, where the primary carbon source is based on fallen leaves and other organic material from the riparian vegetation

(Fisher and Likens, 1972; Vannote *et al.*, 1980). Crayfish affect leaf breakdown (Usio, 2000; Creed and Reed, 2004; Zhang *et al.*, 2004), by converting coarse (CPOM) into fine (FPOM) particulate organic matter (Zhang *et al.*, 2004). These activities and crayfish movements cause an increased dislodgement of sediments (Statzner *et al.*, 2000, 2003; Usio and Townsend, 2004; Statzner and Sagnes, 2008). As a consequence FPOM drift is significantly higher in crayfish presence (Usio *et al.*, 2001) and may serve as a major food source for collecting invertebrates (Mathuriau and Chauvet, 2002).

This hypothesis is strongly supported by our results. Crayfish presence leads to more abundant and diverse collectors, by deriving a surplus of particulate organic matter from leaf shredding (Usio, 2000; Usio *et al.*, 2001; Zhang *et al.*, 2004). This increase in diversity of collectors may have also attracted a more diverse guild of predators (which was the case in all crayfish sites). In contrast, other trophic guilds were suppressed by crayfish. They occupied the ecological niche of shredders and displaced other invertebrate taxa within this guild. Interspecific competition together with predation might have led to significant lower abundances and diversities of shredders in the crayfish streams.

In conclusion, our study strongly indicates that crayfish presence had complex effects at several trophic levels from the food base to predatory consumers. Indigenous stone crayfish as large omnivores play a fundamental role in headwater food webs. A clear understanding of direct and/or indirect interactions in mountain stream ecosystems necessitates a high taxonomic resolution. In this respect, our study is new in considering the aspects above at a larger scale (whole stream experiments) in association with the entire benthic community under natural conditions of pristine headwaters.

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