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Research Paper

Do Predators Condition the Distribution of Prey within Micro Habitats? An Experiment with Stoneflies (Plecoptera)

key words: habitat selection, predator-prey interaction, habitat shift

Abstract

The selection of habitat by macroinvertebrates living in running waters may be influenced by the physical characteristics of the substratum, as well as by the presence of other species. In this study, an artificial river with three different substrata (pebbles, detritus, and leaves) was utilized to analyze the microhabitat preference of two Plecoptera prey species (*Amphinemura sulcicollis* and *Brachyptera risi*), both in absence and in presence of a Plecoptera predator species (*Perla marginata*). In the absence of predators, both prey species showed a clear preference for the leaf microhabitat. When the predators were present, only *Brachyptera risi* showed a change of microhabitat selection, with a decrease of leaves and an increase of pebbles and detritus utilization. *Amphinemura sulcicollis* did not change their substratum utilization. This study demonstrates that the presence of a predator may affect microhabitat selection through a switch from the preferred to the less preferred substrata, although not all species change their habitat utilization in response to predator presence.

1. Introduction

The distribution of benthic invertebrates in lotic systems varies greatly over both large and small spatial scales (VINSON and HAWKINS, 1998). At local scale, many studies have noted the importance of different factors in determining abundance and distribution of organisms in the riverbed, underlining in particular the influence of abiotic elements. Among these, current velocity and substratum characteristics are recognized to be the most important (ALLAN, 1995). Different velocity of flowing waters and the existence of many hydraulic micro-environments shape benthic communities, and determine the presence and allocation of most organisms (STATZNER and HOLM, 1982; BROOKS *et al.*, 2005). Differences in substrate texture and composition play a main role in controlling benthic coenoses. Indeed, some studies found less biological colonisation in fine than in coarse substrates (FENOGLIO *et al.*, 2004). This may reflect their instability, and also some tight packing of sand grains which reduces the trapping of organic detritus and limited the availability of oxygen.

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In riffles, substrate architecture (e.g., stone shapes, sizes and textures) strongly influences the microdistribution of invertebrates (ROBSON and BARMUTA, 1998). Substrate texture has a significant effect on species richness, *i.e.*, more species in rough than in smooth substrates (DOWNES *et al.*, 2000). Another important factor controlling stream invertebrate distribution is the availability of trophic resources, such as submerged macrophytes (HEINO *et al.*, 2003), leaf packs (MURPHY *et al.*, 1998) or coarse particulate organic matter and organic detritus (FENOGLIO *et al.*, 2005).

Apart from these abiotic factors, different biotic elements have strong effects on macroinvertebrate distribution (DUDLEY *et al.*, 1990). Intraspecific competition is an important factor in this frame: PEGEL (1980) demonstrated experimentally that with the increase of benthic density (and consequently competition for space and resources) some species of Diptera Simuliidae increased the tendency to move and enter the drift, and similar findings were found for many other stream invertebrates (BAILEY, 1981). Also interspecific competition could alter microdistribution of stream macrobenthos. For example, HEMPHILL (1988) demonstrated that two stream dwelling filter-feeders (the caddisfly *Hydropsyche oslari* and the blackfly *Simulium virgatum*) were in direct competition for space and shelter; in particular, the presence of the net spinning caddisfly inhibited the occurrence of Simuliids by direct (attacks and aggressive behaviour) and indirect (increased turbulence due to the net architecture) competitive interactions.

Among biotic interactions, predation is supposed to be of great importance in stream systems (PECKARSKY and DODSON, 1980; COOPER *et al.*, 1990). Interestingly, many studies have investigated prey detection mechanisms (e.g., PECKARSKY and PENTON, 1989), diet and feeding preferences (e.g., BO *et al.*, 2008), and functional response (e.g., ELLIOTT, 2003), but less is known about the influence of predators in determining microhabitat selection by prey.

In this context, LANCASTER *et al.* (1991) noticed that the impacts of predators on prey depend on both prey mobility and environmental spatial heterogeneity. Furthermore, ENGLUND (1997) noticed that, at small scales, the main effect of predator presence could be to enhance prey movements and dispersal. In particular, predators can induce an increase in prey emigration rates (SIH *et al.*, 1992, SIH and WOOSTER, 1994).

Some studies investigated the importance of fish predation in determining substrate colonisation by benthic invertebrates. An interesting study of invertebrate prey and vertebrate predators (*Oncorhynchus mykiss*) reported that fish presence had little influence on the diversity or abundance of some insect taxa in different substrates. This study revealed that patterns of substrate colonization could be related to substrate preference (related to surface areas or trapped detritus amounts) rather than to mortality by fish predation (FLECKER and ALLAN, 1984). Similar results were found in another study analysing the impact of Sculpins (*Cottus bairdi*) in determining benthic insect abundance and distribution: the presence of this benthivorous fish had no significant effects on positioning of its invertebrate prey (SOLUK and COLLINS, 1988). These studies indicated a small importance of vertebrate predator in determining benthic invertebrate distribution, but little is known about the importance of invertebrate predators in this context.

In low and mid-order running water systems, Plecoptera represent an important component of the whole benthic community and, among them, Systellognatha stoneflies represent top invertebrate predators (ALLAN, 1983). In this work we utilized an artificial river with three different substrata (pebbles, detritus and leaves) to study the microhabitat preference of two stoneflies prey species. The aims of this study were (a) to observe the microhabitat selection of prey species in the absence of predators, and (b) to examine whether or not the presence of a large sized predator stonefly may result in a change of the preferred microhabitat selection.

2. Methods

2.1. Studied Species

In this experiment we used a predator, *Perla marginata* (PANZER, 1799) (Plecoptera, Perlidae), and two prey, *Brachyptera risi* (MORTON, 1896) (Plecoptera, Taeniopterygidae) and *Amphinemura sulciollis* (STEPHENS, 1836) (Plecoptera, Nemouridae). *P. marginata* is a large-sized predator, with mature nymphs reaching a maximum length of 33 mm (TIERNO DE FIGUEROA *et al.*, 2003) and feeding on a wide range of stream invertebrates, including small and medium sized stoneflies (Bo *et al.*, 2007a). *B. risi* is a medium sized stonefly (8–12 mm, CONSIGLIO, 1980) with a widespread distribution in Europe, and prefers small, forested streams (PUIG, 1984). *A. sulciollis* is smaller, reaching 6.5 mm, and inhabits rhithron throughout Europe (CONSIGLIO, 1980).

The combination of predator and prey species was present in natural conditions, because all organisms were collected in a single and uniform riffle from the same stream reach (Curone Creek, near Fabbria Curone, NW Italy, 44°47'14" N, 9°04'02" E, 620 m a.s.l.). Individuals of the three species were collected in February and March 2008 with a kick-net (500 µm mesh), then transported to the laboratory in a bucket with ice and air pumps, and finally stored in a large and refrigerated artificial stream with oxygenators. Predators were held separately in refrigerated laboratory tanks and starved for three days to standardize hunger levels.

2.2. Experimental Design

We used an experimental stream (200 × 60 × 60 cm), with recirculating water (1200 litres/hour) and controlled temperature (12 °C constant), to simulate natural conditions of Curone Creek. To test habitat preferences, we assembled experimental cages, with a circular shape. The cages were internally separated into three regions of equal area (164 cm²) by small plastic partitions that allowed the passage of organisms (Fig. 1). Each region was randomly filled by a different substratum (approximately 6 cm depth), always collected in the same stream: L – leaves (mainly *Quercus* sp. and *Alnus* sp., with one or two pebbles to prevent floating), P – small pebbles (16 – 32 mm) and D – detritus (fine mixed, inorganic and organic sediments, approximately < 5 mm). These three substrata are common and widespread in the Curone Creek. Organisms could pass from one substratum to another but they could not escape from the cages. We conducted both single species and mixed species substratum-use trials, using simultaneously (a) cages with a single predator, (b) cages with 10 prey, and (c) cages with 10 prey plus a single predator. In predator-prey trials, we began experiments by introducing 10 prey in each cage and then, one hour later, the predator. Each trial was initiated at 16 : 00 h and lasted a single day. At 24 hours after the animals were inserted, we checked all cages, carefully removed the different substrates and recorded the distribution and number of stoneflies.

In a first trial sequence, *B. risi* was the prey species, and we positioned a total of 46 cages: with 10 *B. risi* only (N = 23 cages), and with a *P. marginata* plus 10 *B. risi* (N = 23). In a second trial sequence,

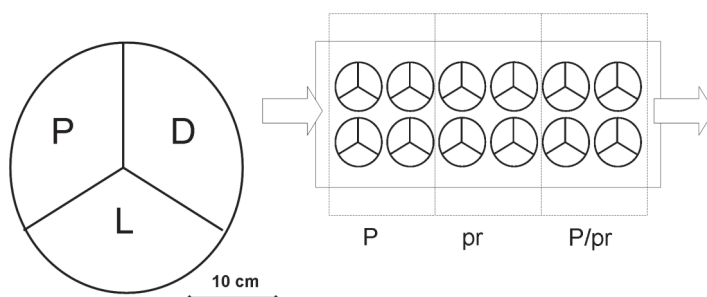


Figure 1. Experimental design and cages. On the left, scheme of a single cage with three microhabitats (P = pebbles, D = detritus and L = leaves). On the right, the artificial stream with 12 cages: in all trials P = predator alone cages, pr = prey only cages, and P/pr = cages containing 1 predator and 10 prey.

A. sulciollis was the prey. We used in total 46 cages: with 10 *A. sulciollis* only ($N = 23$ cages), and with a *P. marginata* plus 10 *A. sulciollis* ($N = 23$). As control, we used cages with *Perla marginata* only ($N = 23$). All specimens were released in the centre of the cage. Densities of stoneflies were within the range usually found in Apenninic lotic environments of the area (Bo *et al.*, 2006, 2007b). We were able to position a maximum of 12 cages in the artificial river, after each 24 hour session. The cages were then cleaned, new substrates were added, and a new session was started.

2.3. Statistical Analysis

Differences between experimental groups (*i.e.*, cages with prey alone, cages with predator alone and cages with prey and predator) were tested by a non-parametric Friedman ANOVA statistics, because the data were not normally distributed. This test is a nonparametric alternative to one-way repeated measures analysis of variance, and it is the most appropriate test for dependent variables, as it is our case. We expected that stoneflies showed substratum preferences, and that these choices could be affected by predator presence. So, the null hypothesis was that there were no differences in prey or predator distribution in the different experimental conditions (prey alone; predator alone; predator plus prey). In this context, the dependent variable was presence of animals in the three substrates, and the independent was the predator presence. All trials were completed in a very short period of time compared with the length of the life cycle of the species, so that time was not considered as a blocking variable. We used a Mann-Whitney U for the assessment of the differences in the number of individuals that were preyed in the trials (with the null hypothesis being that predation was equal in both prey), and also to study differences in the distribution of each species with and without *Perla* (the null hypothesis being that prey distribution was equal with and without predator). Graphs show mean values \pm SE.

3. Results

3.1. Predation Rates

The predator (*P. marginata*) consumed at least one prey organism in most trials (22 of 23 for *B. risi* and 20 of 23 for *A. sulciollis*). Predation was higher in *B. risi* than in *A. sulciollis* cages (Mann-Whitney U = 150.00, $P < 0.01$, $n = 23$, Fig. 2). In the *B. risi* experiment, the consumption ranged from a minimum of 0 to a maximum of 6 individuals/cage, with a mean of 3.08 individuals (± 0.37 SE). In the *A. sulciollis* experiment, predation ranged from 0 to 4 individuals/cage, with a mean of 1.74 individuals (± 0.23 SE).

3.2. *Perla marginata* Substratum Selection

When placed alone, nymphs of *Perla* showed a preference for leaves (Friedman ANOVA = 34.78, $P < 0.001$, $n = 23$, Fig. 3).

3.3. *Brachyptera risi* Substratum Selection

When only *B. risi* nymphs were present in the cages, we detected a statistically significant preference for the leaf substrates (Friedman ANOVA = 18.66, $P < 0.001$, $n = 23$, Fig. 4a). In cages with 10 prey and one predator, *Perla* was almost always found in leaf substrates (Friedman ANOVA = 40.26, $P < 0.001$, $n = 23$), and also *B. risi* showed a significant preference for this substratum (Friedman ANOVA = 16.28, $P < 0.001$, $n = 23$, Fig. 4b). Interestingly, comparing the abundances of prey in the different substrates with or without predators, we detected some significant differences: in leaves, the presence of the predator seemed to act as a deterrent and the presence of *B. risi* decreased (Mann-Whitney U = 115.50, $P < 0.05$,

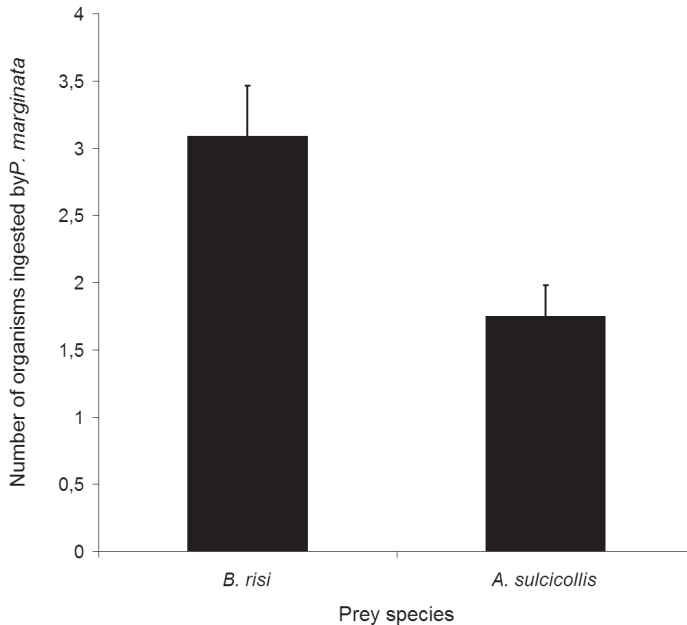


Figure 2. Predation by *P. marginata* in *B. risi* and *A. sulcicollis* cages (mean ± SE).

$n = 23$ – Fig. 6a), though no variations were detected in the selection of the remaining substrates. Neither detritus (Mann-Whitney $U = 183.00$, $P > 0.05$, n.s., $n = 23$) nor pebbles (Mann-Whitney $U = 227.50$, $P > 0.05$, n.s., $n = 23$) were differentially selected when *Perla* was present or absent.

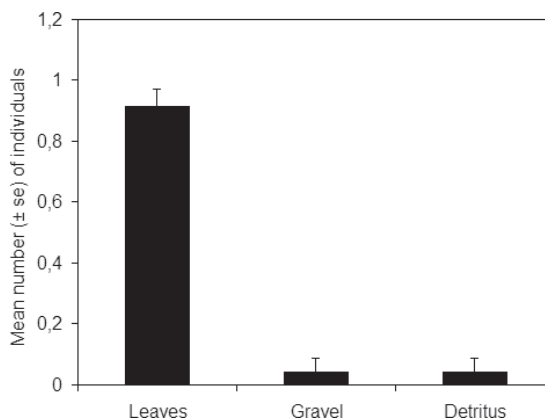


Figure 3. Microhabitat preference of the predator, *P. marginata*.

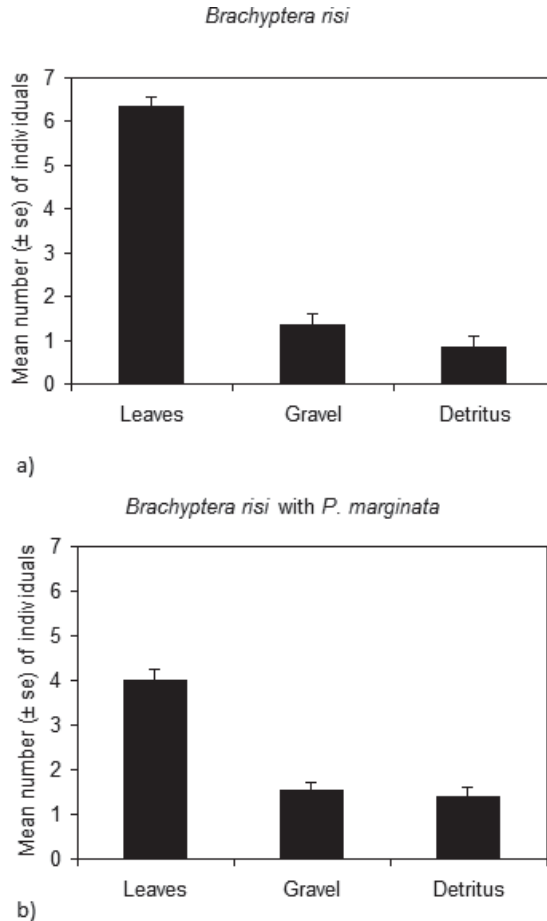


Figure 4. Microhabitat distribution in the *B. risi*/*P. marginata* experimental condition (mean \pm SE).

3.4. *Amphinemura sulcicollis* Substratum Selection

When only *A. sulcicollis* were present, they showed a significant preference for the leaf substratum (Friedman ANOVA = 17.88, $P < 0.001$, $n = 23$, Fig. 5a). In the cages containing predator and prey, leaf substratum was always the most colonized, both by *Perla* (Friedman ANOVA = 23.27, $P < 0.001$) and *A. sulcicollis* (Friedman ANOVA = 20.70, $P < 0.001$, $n = 23$, Fig. 5b). The presence of the predator did not significantly affect the abundance of prey in the three substrata: leaves (Mann-Whitney $U = 220.00$, $P > 0.05$, n.s., $n = 23$, Fig. 6b), pebbles (Mann-Whitney $U = 214.50$, $P > 0.05$, n.s., $n = 23$), and detritus (Mann-Whitney $U = 250.50$, $P > 0.05$, n.s., $n = 23$). In cages without predator, some of the specimens died and were not taken in consideration for data analysis.

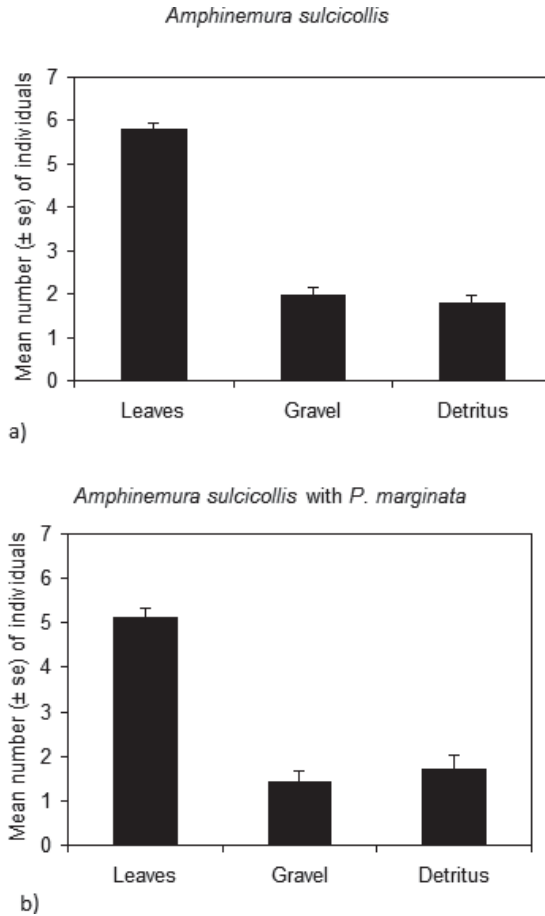


Figure 5. Microhabitat distribution in the *A. sulcicollis*/*P. marginata* experimental condition (mean \pm SE).

4. Discussion

In this study we examined the hypothesis that the presence of a predator could influence habitat selection and micro-distribution of prey. Indeed, a change of habitat utilization in the presence of predators has been reported in several vertebrates (FRASER and CERRI, 1982; DICKMAN, 1992; WERNER *et al.*, 1983) and vertebrate-invertebrate predatory interactions (HARRISON *et al.*, 2005), with a general tendency for prey to switch from optimal to sub-optimal habitats. For instance, a study realized on microdistributions, survival, and drift of stream hydropsychid caddisflies in presence of two predators revealed that the physical presence of stonefly predators drove to the abandonment of some usual refuges, causing an increase in the drift rate of prey (FAIRCHILD and HOLOMUZKI, 2005).

One of the most important elements in predator-prey interaction *i.e.*, prey vulnerability, could be defined as the product of encounter rate and capture probability (PASTOROK, 1981). To explain diet of aquatic predators, encounter rate is supposed to be of greater importance than attack propensity and active predator choice (SIH, 1993; SIH and MOORE, 1990). Encounter rate can be described as the number of prey detected by each predator per unit of time,

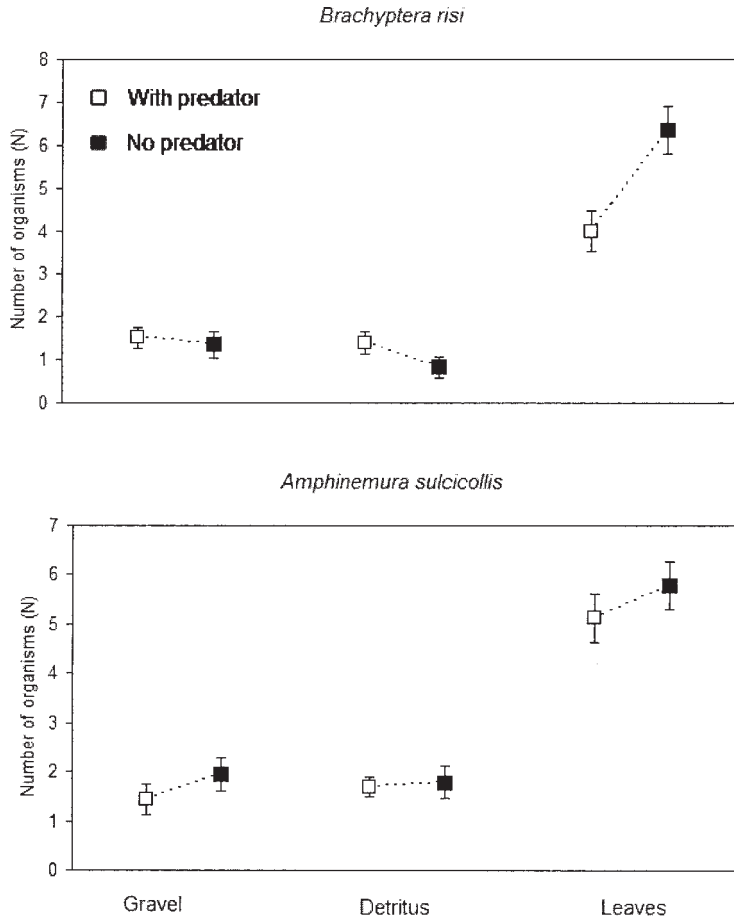


Figure 6. Leaf microhabitat preference in absence and in presence of the predator for *B. risi* and *A. sulcicollis* (mean \pm SE).

and can be calculated as $E.R. = a \times N$, where a is a parameter related to search efficiency and N represents prey density (TURESSON and BRÖNMARK, 2007). In a theoretical model, we can suppose that encounter rate increases proportionally with prey density, but in reality many other factors can also have a strong influence on this.

Search efficiency depends on different factors such as characteristics of predator (*e.g.*, ambusher or searcher strategies) and prey (*e.g.*, the presence of defenses), predator/prey dimensional ratios, and many environmental characteristics (*e.g.*, occurrence and distribution of refuges, water transparency). In field studies, encounter rate is difficult to measure, but in experimental studies encounter rate could be measured directly, through continuous observation or, indirectly, through consumption rates (GREGORY and LEVINGS, 1996). In our study, we controlled some of the factors affecting prey vulnerability, using identical environments and prey density for both prey types. By standardizing these elements, encounter rate was mainly related to morphological and eco-ethological characteristics of predator and prey.

Predator stoneflies forage across the surface of the substrate seeking prey, mainly using their antennae, and they can also use slight hydrodynamic variations to distinguish different

prey types (PECKARSKY and WILCOX, 1989). In natural conditions, prey can avoid predator attacks by utilizing refuges or entering the drift (FAIRCHILD and HOLOMUZKI, 2005), but this second possibility was not allowed in our experimental design, because our study was designed to investigate habitat switching responses. We observed that *P. marginata* showed a higher impact on *B. risi* than on *A. sulcicollis* nymphs. It is likely that encounter rates were higher when both predator and prey shared the same habitat. We noted that, for the three species a leaf microenvironment was preferred over detritus and small pebbles. When alone, *P. marginata*, *B. risi* and *A. sulcicollis* showed a significant positive selection for inhabiting leaves. For this reason, we suspect that the highest impact of the predator on *Brachyptera* could be related not to environmental or ecological factors, but to the larger size of nymphs. *P. marginata* could attack larger prey for two main factors: one factor is that encounters in the leaves section of our cages were probably more frequent with large-sized Brachypterinae than with smaller Nemouridae: predators could face an increased cost to find *A. sulcicollis* because of its smaller size. Indeed, it is known that size can play a main role in increasing encounter per minute (ALLAN and FLECKER, 1988). *A. sulcicollis*, because of its smaller dimensions and scarce mobility, can probably better hide and escape more easily. Another factor is that several studies have demonstrated that Systellognatha carnivorous stoneflies could have a size-based prey selection (ALLAN *et al.*, 1987; MOLLES and PIETRUSZKA, 1987). Our results confirm other studies. The analyses of field feeding habits of *P. marginata* (BO *et al.*, 2007a), *P. bipunctata* (BO *et al.*, 2008) and *P. grandis* (FENOGLIO *et al.*, 2007) also reported a higher preference for medium over small sized prey.

In conclusion, our study shows that the presence of a predator can influence the distribution of benthic invertebrates. The preference of microhabitats may be modified in some but not all species. When the predator *P. marginata* was present, there was a switch from the preferred to the non preferred microhabitats in *B. risi* but not in *A. sulcicollis*. This probably reflects the smaller size of the latter, which contributes to reduced encounter rates and prey vulnerability. It is known that a habitat may sometimes hold more individuals than expected on the basis of its resource (MORRIS, 2005). Our study confirms the hypothesis that the distribution of some prey depends on predation risk as well as resource characteristics. An element of particular interest is that other experimental studies investigated the importance of predation utilizing as models vertebrate predators (generally fish) and invertebrate prey, or invertebrate predator (*e.g.*, alderflies) and prey (*e.g.*, mayflies): our study is one of the first utilizing predators and prey belonging to the same taxonomic group (stoneflies).

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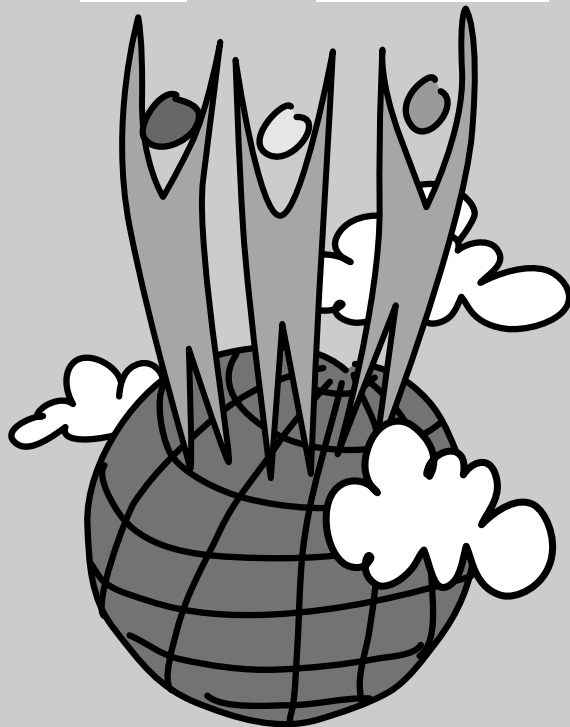
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