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Patch based predation in a southern Appalachian stream

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Streams are characterized by high degrees of patchiness that could influence the role of predators in these systems. Here we assess the impact of predatory benthic fishes on benthic macroinvertebrate density, biomass, and community structure at the patch scale in a fourth order stream in the southern Appalachians. We tested the role of predation in two different patch types: patches inhabited by adult mottled sculpin (*Cottus bairdi*) and random patches. We placed 30 basket pairs (one open to fish predation, and one from which fish predators were excluded) in the streambed at each patch type. We also tested for potential basket effects by setting up a basket control area. Although there was some evidence of basket artifacts on macroinvertebrate density in sculpin patches, these artifacts were not consistent and we do not feel that they affected our results because predators did not affect macroinvertebrate density. In random patches, predation did not significantly affect macroinvertebrate density or biomass. Predators significantly reduced macroinvertebrate biomass in sculpin patches but did not affect prey density. When the data-set was size-limited to exclude macroinvertebrates too large for consumption by sculpin, macroinvertebrate biomass did not differ significantly between exclusion and open baskets. This suggests that sculpin can reduce macroinvertebrate biomass through a combination of consumption and by predator-induced emigration of large macroinvertebrates into areas that are protected from sculpin. In addition, invertebrate predator biomass was higher in predator exclusion baskets in sculpin patches indicating that predation pressure remained high in the exclusion baskets despite fish exclusion. These results illustrate the heterogeneity of streams and the effect of small-scale differences (e.g. location of predators' territories) on local processes. Experiments that utilize these differences can provide insights into these stream processes.

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Predators' affect on the abundance of individual prey taxa or assemblage structure in streams is often inconsistent. Predatory fishes have varied impacts in these systems ranging from strong effects (Dudgeon 1991, Harvey and Hill 1991, Forrester 1994, Englund and Olsson 1996) to few to no effects (Allan 1982, Culp 1986, Dahl 1998a, Dahl and Greenberg 1998). Further, significant predator effects have been found in some habitat types within a system (e.g. riffles) but not in others (e.g. pools, Schlosser and Ebel 1989, Reice 1991, Power 1992), or with benthic fish but not drift feeding fish (Dahl 1998b). In contrast, predator–prey experiments involving invertebrate predators often result in either reduction or emigration of common invertebrate prey (Peckarsky 1985, Walde 1986, Lancaster 1990, Woodward and Hildrew 2002). However, a recent meta-analysis of predator–prey studies in streams did not detect a difference in the efficacy of vertebrate and invertebrate predators, and suggested that the differences between benthic and drift feeding fish may result from a difference in effects on one group of inveretbrate taxa (chironomids, Englund et al. 1999). Predator impact

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models (Cooper et al. 1990, Sih and Wooster 1994) suggest that differences in prey exchange rates may be partially responsible for these variations. In streams, the mesh size of exclosure and/or enclosure cages can influence prey exchange within these experimental units and, therefore, potentially influence experimental results (Cooper et al. 1990, Englund et al. 1999).

Streams consist of a network of heterogeneous habitats on a variety of scales (Frissell et al. 1986, Pringle et al. 1988). Many stream characteristics including substratum, flow, debris, light, organic matter storage, drift, and organism distribution have an inherent level of patchiness. Any of these characteristics may influence the role of predation in the system. For instance, differences in flow regime over two different microhabitats (rock-face and pebble-riffle) can mediate drift, a mechanism of immigration for many smaller macroinvertebrates (Smith-Cuffney and Wallace 1987). On a reach scale, settling rates of drifting invertebrates can be significantly affected by the amount of slow water or "dead zone" area (Lancaster et al. 1996). Therefore, it is not surprising that the immigration of prey through drift may depend on small-scale patchiness in substratum type and flow rates. Further, because prey exchange rates can influence predator impacts, predator–prey dynamics can be affected by small-scale differences in drift.

In response to this physical and biological patchiness, predators also are likely to be patchily distributed in streams (Tokeshi 1994). Thus, predator–prey dynamics in streams also should be spatially heterogeneous. In addition, we would expect that the interactions between predators and prey should be strongest at the scale at which the predators and prey operate, in this case the patch scale (Kotliar and Wiens 1990). For instance, several studies have examined the effects of a patchy distribution of predatory fish within stream pools on prey (Sih et al. 1992, Englund 1999). Although patch choice by fishes has been correlated with the patchy abundance of prey (Petty and Grossman 1996, Petty 1998, Thompson et al. 2001), the effect of heterogeneous prey distribution on a predator's impact has not been examined empirically (Palmer et al. 1996). Moreover, in this particular study stream, feeding patterns of predators vary from territorial fishes, which tend to feed in a defined patch (Petty 1998), to roaming foragers who may disperse their foraging through a larger, less localized area (Thompson et al. 2001). Therefore, the foraging behavior of the predator within a particular patch could create further heterogeneity in the strength of the predator-prey dynamics at the patch scale (Englund 1997).

Our objective was to assess the impact of predatory benthic fishes on benthic macroinvertebrate (hereafter macroinvertebrate) density, biomass, and community structure at the patch scale in Ball Creek, a fourth order stream in western North Carolina. First, we tested whether predation significantly reduced macroinvertebrate prey density or biomass. Second, we asked whether predators affected the abundance of macroinvertebrates in three size classes. Third, we addressed interactions between predators by examining the effect of fish predators on the biomass of invertebrate predators. In order to evaluate the potential effects of differences in ambient foraging pressure, we tested these hypotheses in two different patch types: patches inhabited by adult sculpin and randomly selected patches. We also examined whether our predator exclusion baskets affected macroinvertebrate density and biomass within patches.

Methods

Study site

We conducted this experiment from July to September 1998 in Ball Creek, a fourth order stream at the USDA Forest Service's Coweeta Hydrological Laboratory, Otto, North Carolina. The laboratory is located in the Blue Ridge Province of the southern Appalachian Mountains. Ball Creek contained a mixture of cobble riffles, bedrock and shallow pools typical of many streams in the southern Appalachians. The stream was heavily shaded by a well-developed understory of rosebay rhododendron (*Rhododendron maximum* L.), mountain laurel (*Kalima latifolia* L.) and dogwood (*Cornus florida* L.). Both sites had a fairly simple fish communities consisting of two benthic feeders, mottled sculpin (*Cottus bairdi* Girard) and longnose dace (*Rhinichthys cataractae* Valenciennes) and two drift feeding species, the rainbow trout (*Oncorhynchus mykiss* Walbaum) and brook trout (*Salvelinus fontinalis* Mitchill).

Large predators

Mottled sculpin (*Cottus bairdi*) are small, benthic-feeding fish that are territorial as adults (Petty 1998). They are the most abundant fish in the Coweeta Creek drainage (Freeman et al. 1988) and are found in a variety of stream habitats (Anderson 1985). Sculpin densities averaged 0.5 m^{-2} in the Ball Creek study reaches. In the Coweeta Creek drainage, mottled sculpin can spend 12–13 weeks in a 0.5 m^2 area (Petty and Grossman 1996, Petty 1998). Moreover, patches chosen by sculpin tend to have higher macroinvertebrate biomass than random patches, (Petty and Grossman 1996).

Ball Creek contains one other abundant benthic forager, crayfish (*Cambarus bartonii* Fabricius), and several much less abundant benthic foragers including longnose dace (*R. cataractae*) and three species of salamanders, the two-lined salamander (*Eurycea wilderae* Dunn), the dusky salamander (*Desmognathus fuscus* Green) and the black-bellied salamander

(*D. quadramaculatus* Holbrook). *Cambarus bartonii* (Cambaridae) is a common inhabitant of streams throughout the eastern United States (Pennak 1978). Crayfish densities determined from electrofishing averaged 0.43 m^{-2} in study reaches, although more extensive sampling of crayfish densities in nearby reaches of Ball Creek suggest densities are probably higher (2 m^{-2}, Schofield et al. 2001). Although crayfish are omnivores, crayfish can consume significant amounts of animal material (Momot 1995, Charlebois and Lamberti 1996, Whitledge and Rabeni 1997). Longnose dace is a common riffle-dwelling cyprinid (Jenkins and Burkhead 1994) and is the second most abundant benthic fish in the Coweeta Creek drainage (Freeman et al. 1988). Longnose dace densities averaged 0.11 m^{-2} in the study reaches. Longnose dace primarily feed on macroinvertebrates (Stouder 1990) as they forage over the surface of cobbles and boulders (Thompson et al. 2001). Although all three salamander species feed on macroinvertebrates for at least part of their life cycle, they are not abundant in the lower sections of Ball Creek where fish are present.

Reach characteristics and patch designation

We conducted the experiment during summer baseflow in two 70 m reaches that encompassed riffle, run and pool habitats. The two study reaches were separated by 160 meters. During the study, discharge ranged from 0.05 m^3s^{-1} to 0.76 m^3s^{-1}, with mean daily flow of 0.1 m^3s^{-1}. Substratum in the reaches was a mixture of sand, pebble, cobble and boulder. Habitat, fish densities and macroinvertebrate density and biomass were similar in the two reaches. Therefore, we pooled data from the two reaches for simplicity. Depth ranged from 9 to 38 cm with a mean of 17 cm; wetted width ranged from 3.2 to 5.8 m with a mean of 5.5 m. We identified 30 patches that contained adult territorial sculpin (≥ 5 cm, hereafter identified as sculpin patches). Given their territorial behavior, we assumed that sculpin would continue to reside within the patch. We then used a random number generator to select 30 random patches ≥ 1 m from our sculpin patches. Random patches were chosen to mimic the locations of the observed fish with respect to overall location within the stream and physical characteristics (depth, velocity and substratum composition). We excluded stream sections that were unsuitable as sculpin habitat (Petty 1998). This screening procedure was necessary in order to limit the confounding effect of substratum composition and flow on macroinvertebrates.

To test for habitat differences between the two patch types, we measured depth, mean current velocity and velocity at the stream bed, and visually estimated substratum composition in a 33×22 cm area in the center of the patch. In addition, we measured organic matter standing stock in each patch by placing a stovepipe corer (346 cm^2) into the substratum, removing all coarse particulate organic matter (>1 mm) and then suspended all the fine particulate organic matter. We then subsampled 500 ml of the suspended material, filtered it, and ashed the filter at 500°C for an hour. All measurements were taken one day before the beginning of the experiment. We then compared the physical characteristics of the two patches using principle component analysis (PCA) technique (Grossman and Freeman 1987). Habitat measurements (mean current velocity, bed current velocity, depth, substrate composition, and particulate organic matter) were either log $(x+1)$ or arcsine transformed to avoid heteroskedasticity. We then performed a PCA on measurements collected at random patches. For each significant component (eigenvalue ≥ 1), we scored both the random and sculpin patches to obtain a frequency distribution of scores for each site. The component scores distribution for random and sculpin patches were compared using a χ^2 goodness-of-fit-test (Petty and Grossman 1996). A lack of significant difference in component score distributions between random and sculpin patches, suggests that the physical habitat characteristics of these two patches were not significantly different.

Predation effects

We examined the impact of predators on macroinvertebrate density, biomass, and assemblage structure by placing a pair of substratum-filled baskets ($22 \times 30 \times 10$ cm, 7 mm mesh) in each sculpin ($n = 30$ pairs) and random patch ($n = 30$ pairs). The two patch types differed in their ambient foraging pressure. Baskets in sculpin patches tested for predation effects in patches inhabited by a predator. Baskets in random patches tested for predation effects in patches with unknown levels of predation pressure. Each pair consisted of 1 open basket and 1 basket with a 5 mm mesh hardware cloth cover (open and exclusion baskets respectively). This mesh was small enough to exclude fish, but large enough to allow for immigration and emigration of macroinvertebrates. We buried each basket until the top was flush with the streambed and then filled them with substratum collected from the patch where it was placed. Substratum was first scrubbed clean to remove macroinvertebrates and periphyton. We placed baskets in the stream starting at the most upstream patch in order to minimize the disturbance to the baskets.

Experimental baskets were left in the stream for three weeks (reach 1, July 15–August 5, 1998; reach 2, August 13–September 3, 1998). Baskets were removed starting at the downstream end of each reach to avoid disturbance to the other baskets. Upon removal, baskets were immediately placed in a large plastic bin. We

subsequently removed macroinvertebrates from the substratum by gently scrubbing each of the rocks. Macroinvertebrates were preserved in 10% formalin and stained with rose bengal for later identification. Macroinvertebrates were separated into 2 size classes for identification, > 1 mm and < 1 mm. Due to the large number of macroinvertebrates in the < 1 mm size class, we sub-sampled this size class and identified macroinvertebrates in 1/8 of the sample, in a few exceptionally large samples we used 1/16 of the sample. Macroinvertebrates were identified to genus whenever possible. Chironomids were classified as Tanypodinae or non-Tanypodinae, and macroinvertebrates less than 1 mm in length were identified only to order. Macroinvertebrate body length was measured using a 1 × 1 mm grid and we used length-mass regressions to calculate biomass for each organism (Benke et al. 1999).

We tested for predator effects by comparing mean macroinvertebrate density and biomass between exclusion and open baskets within sculpin and random patches separately. Data for the two patch types were analyzed separately (i.e. one-way ANOVA instead of two-way) because the patches represented two different levels of predation pressure (sculpin presence vs unknown). Samples were checked for homogeneity of variances using Levene's test. We then used a one-way ANOVA to test for significant treatment effects, and, subsequently, if significant overall effects existed, we used linear contrasts to test for predator effects (exclusion baskets vs open baskets). In this case, multiple comparison tests were not appropriate because the comparison of means between the exclusion baskets and basket controls would combine predator and basket effects and therefore not be interpretable. Thus, linear contrasts let us target the comparisons that were interpretable when overall treatment effects were significant. In cases where the data did not meet the assumptions for ANOVA, we used a one-way Kruskal-Wallis to test for overall treatment effects and a non-parametric Tukey-type multiple comparison to test for predator effects if overall effects were significant (Zar 1999). A previous sculpin dietary study in this system showed that they tend not to eat macroinvertebrates of certain genera once the macroinvertebrate attains a certain size (typically > 10 mm, below, Stouder 1990). Consequently, we constructed a size-limited prey data set by limiting the data based on this study (Stouder 1990). In the size-limited data-set all Heptageniidae ≥ 10 mm, Perlidae ≥ 13 mm, Pteronarycidae ≥ 10 mm, and Rhyacophilidae ≥ 10 mm were excluded from the analysis (Stouder 1990). Size-limited prey biomass data were analyzed as described for the total biomass data.

We examined the effects of predators on macroinvertebrate assemblage structure in two ways. First, to determine if large predators affected the distribution of smaller insect predators, we examined whether mean insect predator biomass differed between exclusion and open baskets using two-tailed t tests. The insects were identified as predators based on Merritt and Cummins (1996). However, insects < 1.5 mm were considered generalists and excluded from this analysis. Predatory insects were predominantly predatory stoneflies (Perlidae: *Acroneuria* sp. and Perlodidae: *Isoperla* sp.). Second, we examined the proportion of the assemblage consisting of macroinvertebrates in three different size classes (≤ 1 mm, 1 mm > x < 10 mm, ≥ 10 mm). We chose to analyze the abundance of size classes rather than taxonomic abundance or biomass because we would have had to confine any taxonomic analysis to the order level due to the large number of genera present. Predicting predation effects on macroinvertebrate orders is difficult for two reasons. First, previous diet studies have shown that sculpin consume a variety of dipteran, ephemeropteran, plecopteran, and trichopteran genera (Stouder 1990). Second, different genera within the same order respond differently to predation pressure (Soluk and Collins 1988a). However, the size of the insect may affect its ability to be detected and/or eaten. Very small insects (≤ 1 mm) are smaller then the prey typically captured by sculpin (Hoekstra and Janssen 1985), and very large insects (≥ 10 mm) may not be consumed by the sculpin (Stouder 1990). Therefore, we predicted that predation would be most likely to affect the macroinvertebrates in the middle size class. In addition, our size frequency analysis integrates both density and biomass. We compared the number of macroinvertebrates in a particular size class in exclusion baskets to the number of macroinvertebrates in that size class in open baskets using either a two-tailed t-test or a two-tailed Welch's t-test (Zar 1999).

Basket effects

In order to examine potential basket effects, we established a basket control area adjacent to each pair of baskets. We selected a 346 cm^2 area and removed all substratum within the area to a depth of 10 cm (the depth of the baskets). We gently scrubbed all rocks clean of periphyton and macroinvertebrates and replaced them. This control area can only be considered a partial control in that we could test for differences in having a basket vs. not having a basket, but we could not isolate the effect of the mesh top on the exclusion baskets. At the scale of our baskets (< 1 m), available data suggest that predator impact is controlled by prey migration rather than predator consumption (Englund et al. 2001). Therefore, the cover on the top of the exclusion baskets could be expected to affect prey movement and, therefore, confound our experiment. However, this did not appear to be the case (Discussion). At the end of the experiment, we used a Hess sampler (250 μm mesh) to

collect macroinvertebrates in each basket control area. Macroinvertebrates were preserved in 10% formalin, stained with rose bengal, and identified as described previously for the basket samples.

We tested for basket effects (i.e. significant differences between open baskets vs basket controls) in a manner identical to that used for predator effects. We used one-way ANOVAs to test for overall treatment effects, and, if significant overall treatment effects were present, we subsequently used linear contrast to test for basket effects using both the density and biomass of total and size-limited macroinvertebrates.

Predator impact index

We calculated the Predator Impact Index (PI) of Cooper et al. (1990) for each set of baskets. The $PI = -\ln(N_p/N_c)$ where N_p equaled the number of prey (macroinvertebrates) in open baskets and N_c equaled the number of prey (macroinvertebrates) in the predator exclusion baskets (Cooper et al. 1990). We also calculated predator impact for prey biomass data. We compared the index scores for sculpin and random patches using two-tailed t-tests (Zar 1999).

Observations

To ensure that fish were utilizing open baskets at both the sculpin and random patches, we made observations ($n = 140$) at a subset of the basket pairs. It was more effective to watch the baskets from shore in order to maximize visibility and minimize disturbance due to low water levels. This did limit our ability to observe the basket pairs located in the center of the stream channel. Fish and crayfish were readily visible from the adjacent shore and the observations provided an index of foraging activity in baskets. We noted the presence and type (when possible) of fish or crayfish during each 30-minute observation. Observations were taken on days 5, 6, 10, 11, 14, 15, and 20 of the experiment.

After all macroinvertebrate sampling was complete, we electrofished the study section in order to assess fish populations. We used the three-pass removal method to estimate the populations for fishes and crayfish in both reaches (Freeman et al. 1998).

Results

Habitat data and observations

PCA extracted four significant components from the habitat data. The first component represented the gradient between shallow, higher velocity, erosional patches and deeper, lower velocity, depositional sites (Table 1). There were no significant differences in the PC score distributions between sculpin patches and random patches (Table 1). Sculpin foraging intensity on open baskets in sculpin patches was similar in both reaches; foraging was observed in 42% of the observations. Sculpin were responsible for 59% of those feeding bouts, crayfish were responsible for 18%, and the remaining were unidentified fish. In contrast, we observed foraging in random patches during only 22% of observations. Longnose dace and crayfish were responsible for most of the feeding bouts in the random patches in both reaches. Forty-nine percent of the observed foraging in random patches was by longnose dace and 33% by crayfish.

Baskets effects

Our tests for basket artifacts showed that macroinvertebrate densities were significantly lower in basket control areas compared to open baskets in sculpin patches (Fig. 1), but similar in random patches (Fig. 2). However, biomass was similar in the basket control area and the open baskets and both patch types (Fig. 1, 2). The higher density but similar biomass found in the baskets in sculpin areas suggests that the baskets attracted more small macroinvertebrates in sculpin patches than the basket control area. However, it is unlikely that this artifact affected our results because predators did not affect total macroinvertebrate density (below).

Table 1. Summary of principal component analysis. Significant loadings are presented for each factor. We tested the hypothesis that the distribution of component scores did not significantly differ between sculpin and random patches using a goodness of fit test.

PC factor	Loading	Sculpin vs random patches
1	Depth (−0.72), benthic organic matter (−0.62), sand (−0.33), mean current velocity (0.78), benthic current velocity (0.77), cobble (0.49), boulder (0.25)	$p = 0.84$
2	Sand (−0.56), cobble (−0.54), gravel (0.67)	$p = 0.54$
3	Cobble (−0.049), boulder (0.96)	$p = 0.78$
4	Benthic organic matter (0.53), benthic current velocity (0.5), mean current velocity (0.45)	$p = 0.68$

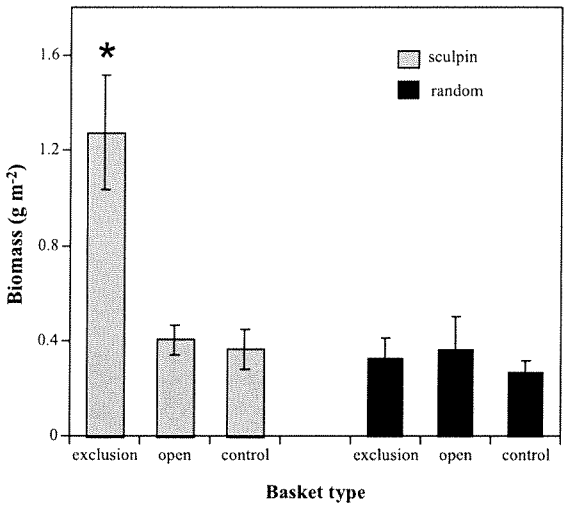

Fig. 1. Macroinvertebrate biomass in the three basket types in sculpin and random patches. We tested for overall treatment effects using one-way ANOVAs in each patch type. We compared the biomass in exclusion baskets to open baskets to test for predation effects using linear contrasts. Significant predation effects ($p < 0.05$) are denoted by an asterik (*) above the exclusion bar. We compared the biomass in open baskets to basket controls to test for basket effects using linear contrasts. Significant basket effects ($p < 0.05$) are denoted by and asterik (*) above the basket control bar. Error bars are ± 1 standard error.

Effect of large predators

At sculpin patches, macroinvertebrate biomass was significantly lower in the open baskets than in the exclusion baskets (Fig. 1). However, large predators (e.g. fish and crayfish) did not significantly affect the density of macroinvertebrates in sculpin sites (Fig. 2). In contrast to total macroinvertebrate biomass, size-limited

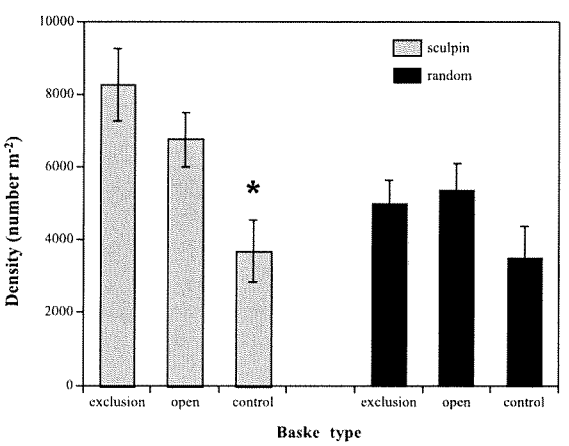

Fig. 2. Macroinvertebrate density in the three basket types in sculpin and random patches. See Fig. 1 for statistical tests and meaning of asteriks. Error bars are ± 1 standard error.

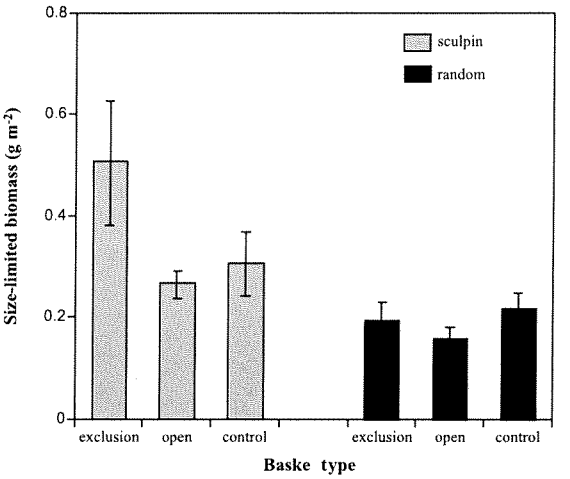

Fig. 3. Size-limited macroinvertebrate biomass in the three basket types in sculpin and random patches. Certain macroinvertebrate species above a certain size (see text) were excluded from this analysis. See Fig. 1 for statistical tests and meaning of asteriks. Error bars are ± 1 standard error.

prey biomass in sculpin patches did not differ between exclusion and open baskets (Fig. 3). This suggests that there were more large macroinvertebrates in the exclusion basket than in the open basket. The biomass of invertebrate predators was significantly greater in exclusion baskets than in open baskets in sculpin patches (Fig. 4). Perlid stoneflies (Perlidae: *Acroneuria* sp.) made up the majority of the invertebrate predators in the baskets, however other predators included predatory caddisflies (Rhyacophilidae: *Rhyacophila* sp.), other perlid stoneflies (Perlidae: *Isoperla* sp.), and a few odonates. At random patches, predators did not sig-

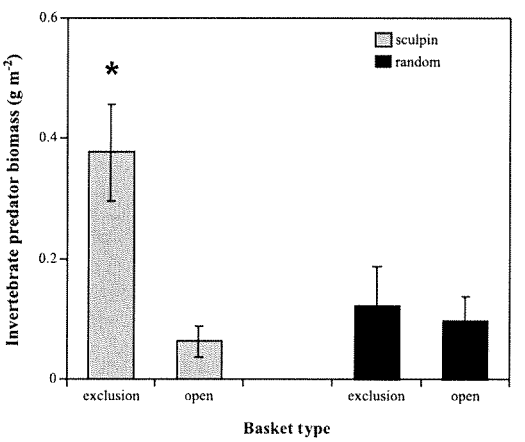

Fig. 4. Invertebrate predator biomass in exclusion and open baskets in sculpin and random patches. We compared the biomass in exclusion and open baskets using Welch's t-tests; significant differences ($p < 0.05$) are denoted with asteriks (*). Error bars are ± 1 standard error.

nificantly affect the density, biomass, or size-limited prey biomass of macroinvertebrates in baskets (Fig. 1–3). In addition, invertebrate predator biomass did not differ significantly between exclusion and open baskets in random patches (Fig. 4).

The density of macroinvertebrates in the three size classes of macroinvertebrates ($\leq$1 mm, 1 mm > x > 10 mm, $\geq$ 10 mm) did differ significantly between exclusion and open baskets in sculpin, but not in random patches. Exclusion baskets in sculpin patches had a higher density of both medium and large macroinvertebrates (Table 2). Although the density of macroinvertebrates in the large size class was small in all baskets, it was three times larger in exclusion baskets in sculpin sites than in any of the other baskets (Table 2).

Predator impact index and swamping

The predator impact index calculated from biomass was higher in sculpin patches (mean+sd; 0.74 ± 1.05) than in random patches (-0.24 ± 1.15) (Welch's t-test, $p = 0.001$). However, there were no significant differences in predator impact scores calculated from density (sculpin, 0.21 ± 0.63; random, -0.15 ± 0.86; Welch's t-test, $p = 0.07$).

Discussion

Predators significantly reduced the biomass of benthic macroinvertebrates in sculpin patches although prey density was unaffected. However, when the data-set was limited to those macroinvertebrates small enough to be consumed by sculpin, biomass did not differ significantly. Predators reduced the density of macroinvertebrates in the medium size class and the large size class. We predicted that predators were likely to have an effect on the distribution of the medium sized insects, because this is the size that sculpin are likely to consume. However, we did not predict the decrease in large macroinvertebrates, which are larger than sculpin typically consume (Stouder 1990). These data suggest that sculpin can reduce macroinvertebrate biomass through a combination of consumption and emigration of large macroinvertebrates. Many of these large macroinvertebrates were predatory stoneflies (Perlidae: *Acroneuria* sp.), which may be partially responsible for the increased invertebrate predator biomass in exclusion baskets. By moving to the exclusion baskets, these large invertebrate predators gain a release from fish predation risk and they increase predation pressure in the exclusion baskets.

In contrast, unknown levels of predation were not strong enough to produce a detectable reduction in biomass or density of macroinvertebrates in open baskets in random patches. Invertebrate predator biomass was similar between open and exclusion baskets in random patches. In addition, the density of small, medium and large macroinvertebrates was similar in the exclusion and open baskets in random patches.

Open baskets in sculpin patches had higher densities of macroinvertebrates compared to basket control areas, but this effect was inconsistent and appeared to have little impact on the outcome of our study because predators did not affect macroinvertebrate densities. However, our basket controls were only a partial control in that we did not isolate the potentially confounding effects of covering the exclusion baskets. It is possible that this cover could have affected the immigration of macroinvertebrates, which would have influenced our results. However, this effect would have been the same in random and sculpin patches, and the density and biomass of macroinvertebrates did not differ significantly between the exclusion and open baskets in random patches. Therefore, it seems more likely that our results reflect the action of predators (particularly sculpin). Several investigators have detected basket effects in stream predation studies (Walde and Davies 1984, Peckarsky and Penton 1990). Baskets can influence macroinvertebrates for a variety of reasons, including increased refuges, changes in flow patterns, and increases in sediment or detritus retentiveness (Peckarsky and Penton 1990).

Sculpin-induced changes in stonefly behavior have been documented by several other researchers (Feltmate et al. 1986, Soluk and Collins 1988b, Schofield 2001). Similar to our findings, the exclusion of sculpin and crayfish via electricity resulted in an increase in pre-

Table 2. Mean density of macroinvertebrates in three size classes in exclusion and open baskets in sculpin and random patches. The density of macroinvertebrates in each size class was compared between exclusion and open baskets in both sculpin and random patches using t-tests or Welch's t-tests.

	Size classes	Exclusion baskets (mean ± sd)	Open baskets (mean ± sd)	DF	t (* Welch's t)	p-value
Sculpin baskets	$\leq$ 1 mm	3700 ± 4193	3626 ± 3342	58	0.075	0.94
	1 < x < 10 mm	3992 ± 2975	2761 ± 1520	43.2	*2.02	0.049
	$\geq$ 10 mm	29 ± 31	6 ± 11	35.9	*3.7	0.0007
Random baskets	$\leq$ 1 mm	2361 ± 2040	3015 ± 2763	56	1.03	0.31
	1 < x < 10 mm	2324 ± 1370	2180 ± 1551	56	0.37	0.71
	$\leq$ 10 mm	7 ± 13	9 ± 15	56	0.53	0.59

datory stonefly biomass on tile substrates (Schofield 2001). Stoneflies select larger stones in the presence of fish (Feltmate et al. 1986). In addition, a perlid stonefly (*Agentina capitata*) spent less time on the top and sides of rocks and was less active in the presence of sculpin (*C. bairdi*, Soluk and Collins 1988b). Predatory stoneflies are capable of consistently reducing the density of prey taxa (Peckarsky 1985). However, the perlid stonefly (*A. capitata*) captured fewer mayflies (*Baetis*) in the presence of sculpin (Soluk and Collins 1988a). Thus, by moving to the exclusion baskets, it is possible that predatory stoneflies were more efficient predators because they could be more active. We assumed that the increase in invertebrate predator biomass alone would indicate that there was higher predation pressure by these invertebrate predators. However, these biomass estimates underestimate the increase in invertebrate predator predation pressure because they do not take into account the potentially increased activity of the predators. This increased invertebrate predator predation pressure may limit our ability to detect fish predation effects (Soluk and Collins 1988a), and may be partially responsible for our inability to detect fish predation effects in the size-limited data-sets when we did find effects on total biomass.

Sculpin inhabit a variety of habitat types (cobble, gravel, and sandy bottom areas of the stream, Petty and Grossman 1996). Previous studies have shown that predation effects can vary with habitat type when the predators use a variety of habitats (Schlosser and Ebel 1989, Reice 1991, Power 1992), but our study suggests that predator effects can vary within a habitat type due to the presence of predators. In addition to habitat type, sedimentation can alter the effectiveness of large predators (predominantly sculpin and crayfish) in Ball Creek (Schofield 2001). Therefore, it is important to consider a variety of factors including habitat type, distribution of predators, and larger scale environmental factors when conducting these types of small-scale experiments.

Our results suggest that predators can affect prey population through both consumption and their interactions with other predators. In sculpin patches, fish exclusion increased both the biomass and potential efficiency of invertebrate predators, thus maintaining high predation pressure on invertebrate prey. In contrast, predation pressure levels in random patches were not strong enough to produce significant effects. These results highlight the patchiness of streams and the effect of small-scale differences on local processes. Moreover, it suggests that these patchy characteristics should be considered when implementing a small-scale experiment in patchy environments such as streams.

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References

Allan, J. D. 1982. The effects of reduction in trout density on the invertebrate community of a mountain stream. – Ecology 63: 1444–1455.

Anderson, C. S. 1985. The structure of sculpin populations along a stream size gradient. – Environ. Biol. Fishes 13: 93–102.

Benke, A., Huryn, A. D., Smock, L. et al. 1999. Length–mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. – J. N. Am. Benthol. Soc. 18: 308–343.

Charlebois, P. M. and Lamberti, G. A. 1996. Invading crayfish in a Michigan stream: direct and indirect effects on periphyton and macroinvertebrates. – J. N. Am. Benthol. Soc. 15: 551–563.

Cooper, S. D., Walde, S. J. and Peckarsky, B. L. 1990. Prey exchange rates and the impact of predators on prey populations in streams. – Ecology 71: 1503–1514.

Culp, J. M. 1986. Experimental evidence that stream macroinvertebrate community structure in unaffected by different densities of coho salmon fry. – J. N. Am. Benthol. Soc. 5: 140–149.

Dahl, J. 1998a. The impact of vertebrate and invertebrate predators on a stream benthic community. – Oecologia 117: 217–226.

Dahl, J. 1998b. Effects of benthivorous and drift-feeding fish on a benthic stream assemblage. – Oecologia 116: 426–432.

Dahl, J. and Greenberg, L. 1998. Effects of fish predation and habitat type on stream benthic communities. – Hydrobiologia 361: 67–76.

Dudgeon, D. 1991. An experimental study of the effects of predatory fish on macroinvertebrates in a Hong Kong stream. – Freshwater Biol. 25: 321–330.

Englund, G. 1997. Importance of spatial scale and prey movements in predator caging experiments. – Ecology 78: 2316–2325.

Englund, G. 1999. Effects of fish on the local abundance on crayfish in stream pools. – Oikos 87: 48–56.

Englund, G. and Olsson, T. 1996. Treatment effects in a stream fish enclosure experiment: influence on predation rate and prey movements. – Oikos 77: 519–528.

Englund, G., Sarnelle, O. and Cooper, D. D. 1999. The importance of data-selection criteria: meta-anlayses of stream predation experiments. – Ecology 80: 1132–1141.

Englund, G., Cooper, S. D. and Sarnelle, O. 2001. Application of a model of scale dependence to quantify scale domains in open predation experiments. – Oikos 92: 501–514.

Feltmate, B. W., Baker, R. L. and Pointing, P. J. 1986. Distribution of the stonefly nymph *Paragnetina media* (Plecoptera: Perlidae): influence of prey, predators, current speed, and substrate composition. – Can. J. Fish. Aquat. Sci. 43: 1582–1587.

Forrester, G. E. 1994. Influences of predatory fish on the drift dispersal and local density of stream insects. – Ecology 75: 1208–1218.

Frissell, C. A., Liss, W. J., Warren, C. E. et al. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. – Environ. Manage. 10: 199–214.

Freeman, M. C., Crawford, M. K., Barrett, J. C. et al. 1988. Fish assemblage and stability in a southern Appalachian stream. – Can. J. Fish. Aquat. Sci. 45: 1949–1958.
Grossman, G. D. and Freeman, M. C. 1987. Microhabitat use in a stream fish assemblage. – J. Zool. 212: 151–176.
Harvey, B. C. and Hill, W. R. 1991. Effects of snails and fish on benthic invertebrate assemblages in a headwater stream. – J. N. Am. Benthol. Soc. 10: 263–270.
Hoekstra, D. and Janssen, J. 1985. Non-visual feeding behavior of the mottled sculpin, *Cottus bairdi*, in Lake Michigan. – Environ. Biol. Fishes 2: 111–117.
Jenkins R. E., and Burkhead, N. M. 1994. Freshwater fishes of Virginia. – Am. Fish. Soc., Bethesda, Maryland.
Kotliar, N. B. and Wiens, J. E. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. – Oikos 59: 253–260.
Lancaster, J. 1990. Predation and drift of lotic macroinvertebrates during colonization. – Oecologia 85: 48–56.
Lancaster, J., Hildrew, A. G. and Gjerlov, C. 1996. Invertebrate drift and longitudinal transport processes in streams. – Can. J. Fish. Aquat. Sci. 53: 572–582.
Merritt, R. W. and Cummins, K. W. 1996. Aquatic insects of North America. – Kendall/Hunt Publishing Company.
Momot, W. T. 1995. Redefining the role of crayfish in aquatic ecosystems. – Rev. Fish. Sci. 3: 33–63.
Palmer, M. A., Allan, J. D. and Butman, C. A. 1996. Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. – Trends Ecol. Evol. 11: 322–326.
Peckarsky, B. L. 1985. Do predaceous stoneflies and siltation affect the structure of stream insect communities colonizing enclosures? – Can. J. Zool. 63: 1519–1530.
Peckarsky, B. L and Penton, M. A. 1990. Effects of enclosure on stream microhabitat and invertebrate community structure. – J. N. Am. Benthol. Soc. 9: 249–261.
Pennak, R. W. 1978. Freshwater invertebrates of the United States. 2nd ed. – Wiley.
Petty, J. T. 1998. Mottled sculpin in a dynamic landscape: linking environmental heterogeneity, individual behaviors, and population dynamics in a southern Appalachian stream. – PhD thesis, Univ. of Georgia.
Petty, J. T. and Grossman, G. D. 1996. Patch selection by mottled sculpin (Pisces: Cottidae) in a southern Appalachian stream. – Freshwater Biol. 35: 261–276.
Power, M. E. 1992. Habitat heterogeneity and the functional significance of fish in river food webs. – Ecology 73: 1675–1688.
Pringle, C. M., Naiman, R. J., Bretschko, G. et al. 1988. Patch dynamics in lotic systems: the streams as a mosaic. – J. N. Am. Benthol. Soc. 7: 503–524.
Reice, S. R. 1991. Effects of detritus loading and fish predation on leafpack breakdown and benthic macroinvertebrate communities in Quebec, Canada. – Can. J. Zool. 64: 1930–1936.
Schlosser, I. J. and Ebel, K. K. 1989. Effects of flow regime and cyprinid predation on a headwater stream. – Ecol. Monogr. 59: 41–57.
Schofield, K. A. 2001. Top-down interactions in southern Appalachian streams: an examination of temporal and spatial variability. – PhD thesis, The Univ. of Georgia.
Schofield, K. A., Pringle, C. M., Meyer, J. L. et al. 2001. The importance of crayfish in the breakdown of rhododendron leaf litter. – Freshwater Biol. 46: 1191–1204.
Sih, A. and Wooster, D. E. 1994. Prey behavior, prey dispersal, and predator impacts on stream prey. – Ecology 75: 1199–1207.
Sih, A., Kats, L. B. and Moore, R. D. 1992. Effects of predatory sunfish on the density, drift, and refuge use of stream salamander larvae. – Ecology 73: 1418–1430.
Smith-Cuffney, F. L. and Wallace, J. B. 1987. The influence of microhabitat on availability of drifting invertebrate prey to a net-spinning caddisfly. – Freshwater Biol. 17: 91–98.
Soluk, D. A. and Collins, N. C. 1988a. Synergistic interactions between fish and stoneflies: facilitation and interference among stream predators. – Oikos 52: 94–100.
Soluk, D. A. and Collins, N. C. 1988b. A mechanism for interference between stream predators: response of the stonefly *Agnetina capitata* to the presence of sculpins. – Oecologia 76: 630–632.
Stouder, D. J. 1990. Dietary fluctuations in stream fishes and the effects of benthic species interactions. – PhD thesis. Univ. of Georgia.
Thompson, A. R., Petty, J. T. and Grossman, G. D. 2001. Multiscale effects of resource patchiness on foraging behavior and habitat use by longnose dace, *Rhinichthys cataractae*. – Freshwater Biol. 46: 145–160.
Tokeshi, M. 1994. Community ecology and patchy freshwater habitats. – In: Giller, P. S., Hildrew, A. G. and Raffaelii, D. G. (eds), Aquatic ecology: scale pattern, and process. Blackwell, pp. 63–92.
Walde, S. J. 1986. Effects of an abiotic disturbance on a lotic predator–prey interaction. – Oecologia 69: 243–247.
Walde, S. J. and Davies, R. W. 1984. Invertebrate predation and lotic prey communities: evaluation of in situ enclosure/exclosure experiments. – Ecology 65: 1206–1213.
Whitledge, G. W. and Rabeni, C. F. 1997. Energy sources and ecological role of crayfishes in an Ozark stream: insights from stable isotopes and gut analysis. – Can. J. Fish. Aquat. Sci. 54: 2555–2563.
Woodward, G. and Hildrew, A. G. 2002. The impact of a sit-and-wait predator: separating consumption and prey emigration. – Oikos 99: 409–418.
Zar, J. H. 1999. Biostatistical analysis, 4th ed. – Prentice-Hall International, Inc.