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Authors

Lovell, James A

Fletcher, Dean E

Cooper, Scott D

et al.

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Fish predation and macroinvertebrate abundance on snags in low-gradient blackwater streams

James A. Lovell^{1,2}, Dean E. Fletcher^{1,3}, Scott D. Cooper^{2,4}, and J Vaun McArthur^{1,5}

¹Savannah River Ecology Laboratory, Drawer E, Aiken, South Carolina 29802 USA

²Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California USA 93106

Abstract: Investigations into how fish affect macroinvertebrates in lotic ecosystems have produced equivocal results, and few researchers have examined fish effects on invertebrates in sandy-bottomed blackwater streams. We measured the responses of macroinvertebrate density, biomass, and body size to varying levels of fish predation on snags in 2 southeastern USA blackwater streams. We manipulated fish densities in 3 large enclosures (46–64 m²) in each of 2 streams and included treatments without fish (0X = control), with fish at ambient density (1X), and with fish at 2× ambient density (2X). Macroinvertebrates in enclosures were sampled using 20 tag alder (*Alnus serrulatus*) snags, ½ of which were allowed to colonize for 2 wk (colonizing community) and ½ for 2 mo (established community). Increasing invertivorous fish biomass resulted in a significant decrease in total macroinvertebrate density, but not macroinvertebrate biomass, in both types of communities (colonizing and established). We found that the biomass of invertivorous fish was a better predictor of prey responses to manipulations than total fish biomass or density. We conclude that high fish levels can significantly reduce the density of macroinvertebrate prey in southeastern blackwater streams. We attribute this effect to prey vulnerability to a diverse assemblage of stream fishes that prey selectively on small invertebrates.

Key words: fish predation, macroinvertebrates, blackwater streams, snags, sandy-bottomed

Macroinvertebrates are a primary food resource for many species of freshwater fish, and macroinvertebrate communities can be shaped by fish predation. Some investigators have found strong effects of native and nonnative fishes on stream macroinvertebrate communities (Dahl 1998, Williams et al. 2003, Baxter et al. 2004, Burra et al. 2007, Kadye et al. 2013, Rodríguez-Lozano et al. 2015), whereas others have reported effects that vary over prey and predator species and environmental conditions (Dahl 1998, Gibson et al. 2004, Winkelmann et al. 2007). Still others have found no significant effects of fish on invertebrate community structure or abundance (Bertrand et al. 2013). Fish have variable effects on invertebrate drift composition (Forrester 1994, Winkelmann et al. 2008) and variable indirect effects on leaf decomposition rates (Ruetz et al. 2002, 2006, Woodward et al. 2008, Hermann et al. 2012), periphyton abundance (Power 1992, Dahl 1998, Forrester et al. 1999, Kurlle and Cardinale 2011, Shelton et al. 2015), and terrestrial–freshwater linkages (Baxter et al. 2004) via their effects on invertebrates. Other investigators have documented variable effects of fish species introductions or losses on freshwater communities (Herbst et al. 2009, Lepori et al. 2012, Holitzki et al. 2013, Kadye et al.

2013). Some of the inconsistencies among the results of past studies may be a consequence of variation in the spatial and temporal scales, design, analysis, and interpretation of experiments (Cooper et al. 1990, Englund et al. 2001). Nevertheless, some of this variation in results is undoubtedly caused by true differences in the effects of fish on prey in environments with differing fish and invertebrate assemblages and abiotic conditions.

Many studies of the effects of predatory fish have been conducted in northern or high-elevation, clear streams with moderate-to-high gradients, coarse substrata, and low fish species diversity (McAllister et al. 1986, Vimos et al. 2015). In contrast, few authors have investigated the effect of fish predation on benthic macroinvertebrates in low-gradient, blackwater systems, such as those draining the southeastern Coastal Plains of the USA. Fish species diversity in this geographical region can be 4 to 8× higher than in the western USA (McAllister et al. 1986, Marcy et al. 2005). Within and among broad geographic regions, increased species richness tends to be associated with greater niche and ecomorphological diversification, which in turn influence use and partitioning of resources by fish assemblages (Winemiller

E-mail addresses: ²Present address: Confluence Consulting, Inc., 211 North Grand Avenue, Suite E, Bozeman, Montana 59715 USA, jlovell@confluenceinc.com; ³fletcher@srel.uga.edu; ⁴scott.cooper@lifesci.ucsb.edu; ⁵To whom correspondence should be addressed, mcarthur@srel.uga.edu

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1991). In these shifting, sandy-bottomed streams, submerged woody debris and root mats are the only hard, stable substrata available for invertebrate colonization. The sandy bottom does harbor some invertebrate taxa, but dominant fishes (percids [darters], cyprinids [minnows], and centrarchids [sunfishes]) prey primarily on drifting macroinvertebrates or those associated with snag habitats (Marcy et al. 2005). Snags have been identified as the most biologically diverse and productive habitat per unit surface area in these sandy-bottomed streams, where they can host macroinvertebrate densities >5000 individuals (ind)/m² (Benke et al. 1984, Thorp et al. 1985). Prey on snags are especially vulnerable to fish predators because snags are hard substrata suspended in the stream current. This position allows invertivorous fish to feed from any direction.

Given the high abundance and species diversity of fishes in coastal-plain streams and the potential vulnerability of snag-dwelling prey to fish, we hypothesized that fish predation would substantially reduce invertebrate density, biomass, and body size on snags. We tested these hypotheses by monitoring the responses of colonizing and established invertebrate snag communities to manipulated fish densities in large field enclosures.

METHODS

Study sites

We elected to work in 5 blackwater tributaries (3rd-order) of Tinker Creek, on the US Department of Energy's Savannah River Site (SRS), a large (800 km²) National Environmental Research Park in the upper coastal plain of South

Carolina. We set up large enclosures to accommodate 3 experimental treatments, including no, ambient, and 2× ambient density fish, in each stream. However, a storm destroyed our study enclosures in 3 of the streams and forced us to remove them from our study. Enclosures remained intact in Millstone Branch and Poison Ivy Creek, allowing us to collect the data that form the basis for our paper. These 2 streams are 3rd-order, spring-fed, sandy-bottomed, blackwater streams characterized by abundant coarse woody debris and scattered deposits of fine and coarse organic matter. The fish fauna is dominated by cyprinids with drift-feeding shiners (*Notropis* spp.) having the highest density in both systems (Table S1). Both streams are ~1.7 m wide with a mean water temperature of 19.5°C. Mean current velocity is 0.08 m/s in Millstone Branch and 0.13 m/s in Poison Ivy Creek. A mostly closed canopy of mixed hardwoods (*Quercus* spp., *Carya* spp., and *Liquidambar styraciflua*, among others) and pine (*Pinus* spp.) typical of southeastern USA bottomland forests characterizes the riparian vegetation. Selective timber harvesting in upland areas is one of the few disturbances to have occurred in these tributary drainage basins over the last 50 y.

Experimental enclosures

We manipulated fish densities in 3 enclosures in each stream between June and September 1988 (Fig. 1). Each enclosure consisted of an up- and downstream 1-m-high, 1.3-cm-mesh hardware-cloth fence erected across the stream channel. We drove 2-m steel posts 1 m into the sediment to support the fences. Fence bottoms were buried ~20 cm be-

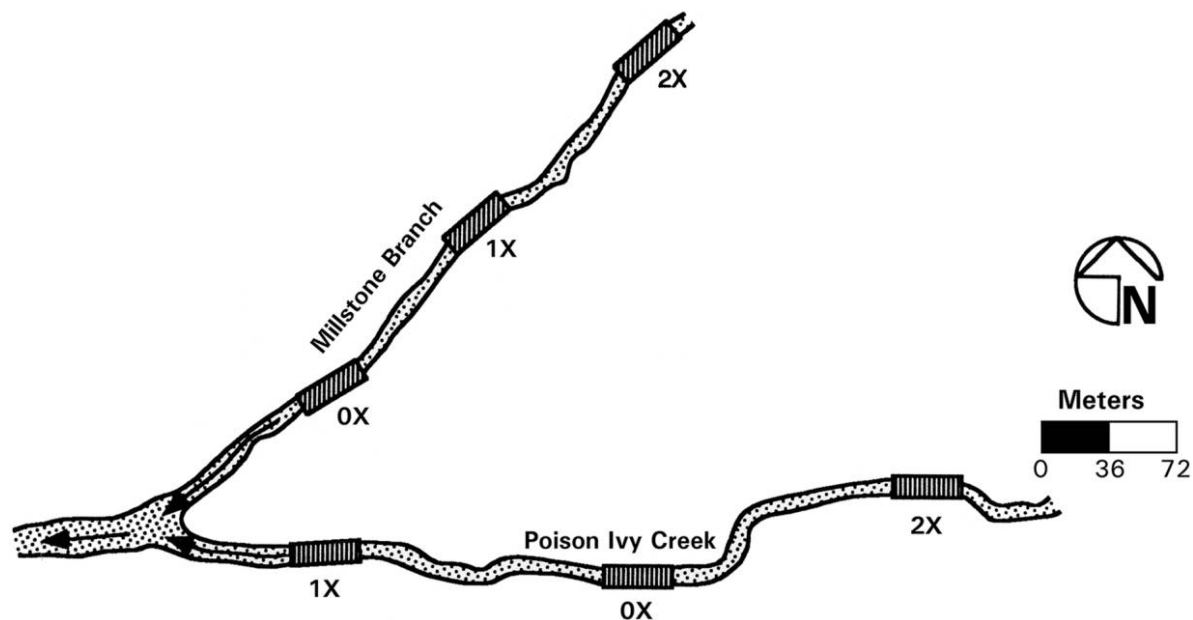


Figure 1. Illustration of the 2 study streams, Millstone Branch and Poison Ivy Creek, used in the experiment. Striped blocks indicate approximate locations of enclosures. Numbers beside each enclosure represent the density of fish added to that enclosure (0X = fish removal, 1X = natural fish density, and 2X = 2× natural fish density).

low the streambed surface, and both ends were embedded ≥ 50 cm into the banks. A skirt of 2-m-wide fiberglass window screen was stitched to the bottom of the hardware cloth fences, stretched upstream, then covered with sandbags and loose sand to prevent scouring and fish passage beneath the hardware cloth. In addition, we attached a layer of 0.32-cm-plastic mesh to the upstream side of the hardware cloth to decrease the mesh size of each fence. After construction, we removed detritus daily from the upstream side of each fence and placed it on the downstream side to allow the passage of this material through enclosures.

Englund et al. (2001) concluded that stream experimental arenas that were 15 to 35 m in length constituted large-scale experimental units where prey responses to predators were driven primarily by consumption by predators. The length of each enclosure (~ 34 m long) in our study was $\sim 20\times$ the mean channel width and encompassed all dominant stream habitats (Table 1). Enclosures were separated by ≥ 40 channel widths to minimize exchange between treatments. These relatively large enclosures were chosen to minimize edge effects and to reduce the risk that any decline in macroinvertebrate numbers might be masked by immigration from nearby untreated areas (Englund et al. 2001). Furthermore, the enclosures were several times longer than the average drift distance recorded for most macroinvertebrates (Elliott 2003).

Fish manipulations

Our fish density manipulations included 3 treatments (1/enclosure) in each stream: fish removal (0X), all fish species at ambient densities (1X), and all fish species at double ambient densities (2X). We defined ambient den-

sity as the density of fish prior to manipulation averaged across all enclosures in a stream. Each stream was considered a block, and treatments were randomly assigned to each enclosure within each block (Fig. 1).

We estimated fish density and community composition by making 3 passes through each enclosure with a backpack electroshocker (Model 15-A; Smith–Root, Vancouver, Washington). A pass consisted of slowly moving upstream while shocking all available habitat including both shorelines and the entire bottom surface area. Three passes were always sufficient to deplete the fish population, so electrofishing efficiency was assumed to be similar on all sampling dates. We removed all fish from the 3 enclosures within a stream, placed them in aerated coolers, and identified and measured (total length) each fish. We restocked $\frac{1}{3}$ of all fish collected in the 1X fish enclosure and the remaining $\frac{2}{3}$ in the 2X fish enclosure with care taken to maintain similar species composition among enclosures. No fish were returned to the 0X fish enclosure. We replaced fish accidentally killed during stocking of the enclosures with individuals of the same species and similar size from stream reaches downstream of the study site.

At the conclusion of the experiment (38 d), we collected fish from each enclosure by electroshocking as described above, and identified, measured, and returned them to the stream. We calculated fish biomass from length data measured from fish collected during stocking and recovery, and length–mass regression equations published by Bennett and McFarlane (1983) and unpublished data collected by J. Aho (SRS). We also assigned each fish species to piscivore or invertivore feeding guilds following Bennett and McFarlane (1983).

Table 1. The enclosure length, mean stream wetted width and depth, current velocity, and relative snag area for each treatment enclosure in each study stream. Relative snag area was computed as estimated snag area divided by estimated stream bottom area. Density and biomass are shown for fish stocked and recovered from each enclosure. Ind = individuals.

Variable	Fish treatment					
	Millstone Branch			Poison Ivy Creek		
	0×	1×	2×	0×	1×	2×
Enclosure length (m)	33.8	34.2	34.4	30.2	30.6	31.4
Mean width (m)	1.62	1.86	1.70	1.54	1.85	1.70
Mean depth (m)	0.13	0.17	0.23	0.10	0.10	0.07
Current velocity (m/s)	0.10	0.09	0.06	0.14	0.14	0.10
Relative snag area (m ² /m ²)	0.271	0.154	0.126	0.151	0.416	0.414
Density fish stocked (ind/m ²)	0	1.73	3.51	0	1.34	2.76
Density fish recovered (ind/m ²)	0.40	0.63	1.57	0.62	1.32	1.41
Biomass fish stocked (g/m ²)	0	4.87	8.86	0	2.40	6.11
Biomass fish recovered (g/m ²)	3.80	3.40	5.81	1.71	2.66	4.42

Macroinvertebrate sampling

We collected invertebrates with snag samplers, each consisting of a 20-cm-long, 5–7-cm-diameter tag alder stem with a mean total surface area of ~ 400 cm². These samplers were less complex than most natural snags, but they allowed us to standardize the size, shape, orientation, depth, stage of conditioning, and colonization time of sampling units. We fastened samplers to a plastic pipe stake driven into the sediment near naturally occurring snags with the same alignment as the nearest natural snag. We placed 10 snag samplers in each enclosure and allowed colonization to proceed for ~ 61 d (established samples) before manipulating fish densities within the enclosures. We exposed snag samplers to fish treatment densities for an additional 38 d. We introduced a 2nd set of 10 snag samplers into each enclosure at the beginning of the fish manipulation, and sampled them after 15 d to measure the effects of fish predation on colonizing macroinvertebrates (colonizing samples). We collected snag samplers by enclosing them in a 0.25-mm-mesh net and preserved them and the contents of the net in 95% ethanol. We returned the samplers and the contents of the nets to the laboratory where snags were rinsed and gently scrubbed to dislodge invertebrates. We passed the resulting slurry through a 0.25-mm-mesh sieve (No. 60 US Standard), preserved the invertebrates in vials with 95% ethanol, and measured the surface area of the snag sampler. We identified all macroinvertebrates to the lowest possible taxonomic level (usually genus), assigned them to a functional feeding group (Merritt and Cummins 1984), and measured their head widths and body lengths with the aid of an image analysis system (Mocha 1.2; Jandel Scientific, San Rafael, California). We converted length measurements to biomass based on length–biomass regressions (Smock 1980). We did not estimate mass for members of the Bivalvia, Gastropoda, Hydracarina, Nematoda, or Oligochaeta because these organisms were rare. Density and biomass estimates were calculated as ind/m² and mg/m² sampling snag surface area, respectively.

Colonizing invertebrates were sampled near the beginning of the experiment, so we examined relationships between colonizing invertebrate abundance and the number and biomass of fish initially stocked in each enclosure. In contrast, we compared established invertebrate community samples taken at the end of the experiment to the number and biomass of fish recovered from each enclosure at the end of the experiment (Table 1).

Statistical analysis

We calculated invertebrate density, biomass, and body size for each snag sampler and averaged them across the 10 colonizing or 10 established samplers from each enclosure. We used enclosure means as replicates in statistical analyses ($n = 6$), with 3 treatments (0X, 1X, and 2X fish density) distributed within each of 2 streams. We treated

invertebrate density, biomass, or body size as response variables; streams as blocks; and treatments (0X, 1X, and 2X fish) as the independent variable in analyses of variance (ANOVAs) followed by Tukey's Honestly Significant Difference (HSD) pairwise treatment comparisons. Fish density and biomass in the enclosures changed during the experiment (Table 1), so we also examined relationships between invertebrate variables and fish density or biomass with regression analyses ($n = 6$).

RESULTS

Fish manipulations

Fish density and biomass stocked in each enclosure were near treatment targets (Table 1). Fish densities in enclosures, however, did not remain constant over the course of the experiment because of unpredictable local storms that caused flooding, fish movement, and mortality (Fig. 2A). Nevertheless, the ranking of fish density for each treatment (0X < 1X < 2X) remained the same for both streams throughout the experiment, and fish density in the 2X treatment remained 2 to 3 \times the density in the 0X treatment (Table 1). The number of fish in the 2X enclosures in both streams reverted to the natural density of fish found before the experiment, but fish density in the 1X enclosure in Millstone Branch declined through the experiment.

Treatment effect

Total density, but not biomass, of invertebrates was marginally or significantly affected by fish in colonizing (ANOVA, $p = 0.08$) and established communities (ANOVA, $p = 0.04$) (Fig. 2B, C). Across treatments, the density of invertebrates in the 2X fish treatment was significantly lower than the density of invertebrates in the no fish (0X) treatment (Tukey's HSD, $p < 0.025$ for both colonizing and established communities), but invertebrate density did not differ between the 0X and 1X fish treatments for either colonizing or established communities.

Relationships between invertebrate density and total fish density, total fish biomass, and invertivorous fish density were not significant (linear least-squares regression, $p > 0.05$). However, invertebrate density and invertivore biomass in colonizing ($R^2 = 0.71$, $p = 0.04$) and established ($R^2 = 0.90$, $p = 0.004$) communities decreased significantly as invertivore fish biomass increased (Fig. 3). In addition, the mean mass of individual macroinvertebrates increased significantly as the biomass of invertivores increased for established ($R^2 = 0.85$, $p = 0.009$; Fig. 4A) but not for colonizing ($R^2 = 0.09$, $p = 0.57$; Fig. 4B) communities.

Direct comparisons between the colonizing and established invertebrate communities are difficult to make because they were exposed to predation for different lengths of time. Nevertheless, the relationship between invertebrate density and invertivore biomass appeared to differ between colonizing and established communities (Fig. 3).

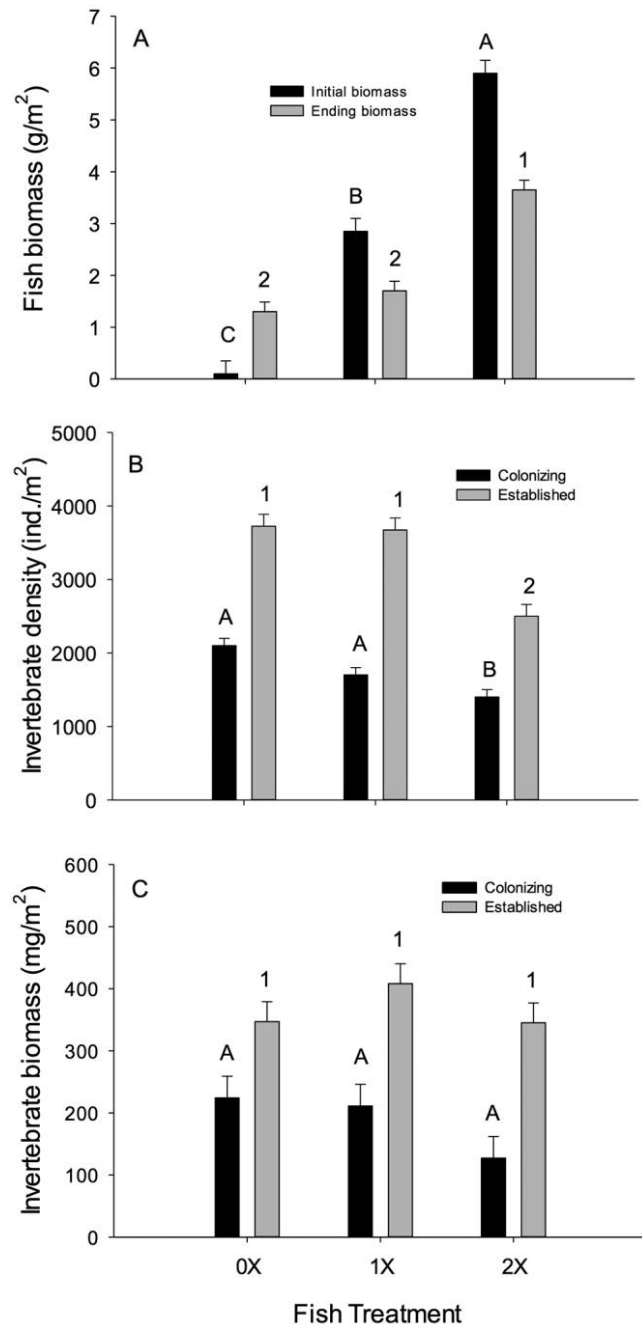


Figure 2. Mean (+SE) initial and ending biomass of invertivorous fish (A), and macroinvertebrate densities (B) and biomass (C) on colonizing and established snags in each fish treatment (0X = fish removal, 1X = natural fish density, and 2X = 2× natural fish density). Bars with the same letters or numbers are not significantly different (Tukey's Honestly Significant Difference, $p > 0.05$). Ind = individuals.

The larger negative slope of the invertebrate vs fish regression for established ($m = -662$) than for colonizing ($m = -116$) communities suggests that predation effects were stronger on established than colonizing communities.

DISCUSSION

Treatment effects

Past investigations of the effect of predatory fish on stream invertebrate communities have produced equivocal results, possibly because of variability in predator or prey identity or density, enclosure size and permeability, current velocities, or substratum sizes. Many studies were conducted primarily with salmonid fish in stony streams, and their authors reported variable effects on invertebrate prey (Allan 1982, Reice 1983, Flecker and Allan 1984, Culp 1986, Reice and Edwards 1986, Dahl 1998, Englund et al. 2001). In contrast, authors reported significant fish effects on prey for most studies done with species other than salmonids, e.g., Mottled Sculpins (*Cottus bairdi*), Creek Chubs (*Semotilus atromaculatus*), Rosyside Dace (*Clinostomus funduloides*), other cyprinids, and introduced poeciliids (Flecker 1984, Koetsier 1989, Gilliam et al. 1989, Reice 1991, Schlosser and Ebel 1989, Holitzki et al. 2013, Rodríguez-Lozano et al. 2015).

In our study, increasing invertivorous fish biomass significantly reduced the densities of colonizing and established macroinvertebrates on snags. Thus, fish predation can affect invertebrate populations on snags in southeastern blackwater streams. In contrast, Herbst et al. (2009) found similar total macroinvertebrate densities in trout and fishless stony streams in California's Sierra Nevada, although trout did affect individual taxa. In streams with stony substrata, high spatial heterogeneity limits the effects of predation by providing more refugia for prey than simpler systems such that burrowing or cryptic prey can avoid surface or water-column predators by seeking interstitial refugia (Flecker and Allan 1984, Gilliam et al. 1989, Power 1992, Diehl et al. 2000, Rosenfeld 2000, Meissner and Muotka 2006). In contrast, highly productive, complex debris dams in blackwater, sandy-bottomed streams can in-

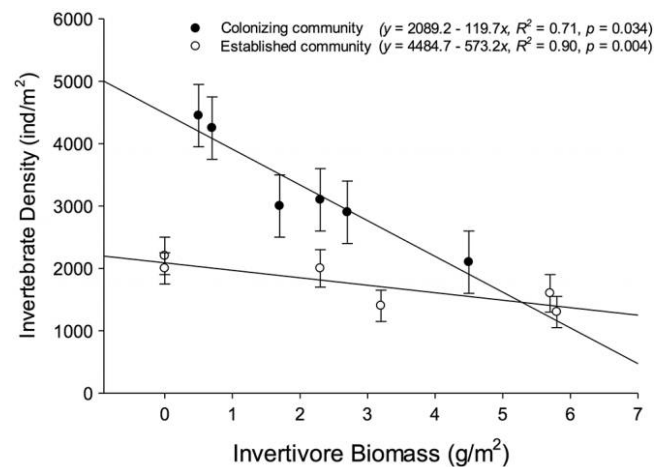


Figure 3. Relationship between macroinvertebrate density and invertivore biomass for colonizing and established invertebrate communities. Ind = individuals.

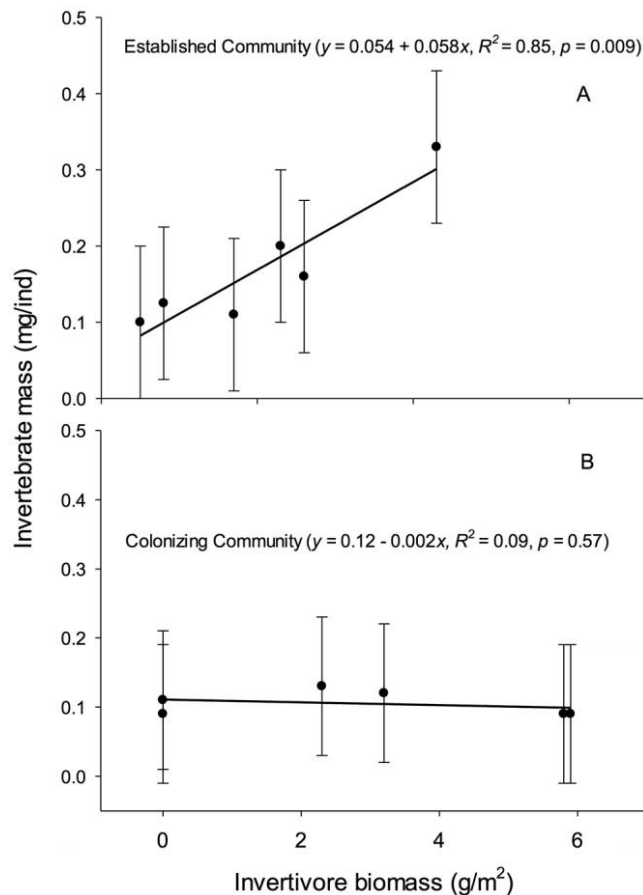


Figure 4. Relationship between average individual body mass of snag invertebrates and invertivore biomass for established (A) and colonizing (B) invertebrate communities. Ind = individual.

crease available niches and refugia for macroinvertebrates, but also increase the local abundances of fish that use these habitats (Everett and Ruiz 1993, Monzyk et al. 1997). Predator foraging efficiency and effects on exposed invertebrates may be high because prey on snags are exposed to benthic and water-column fish predators from all angles. Furthermore, fish species diversity in these blackwater systems is high. Different fish species prey on drifting, emerging, epifaunal, and interstitial prey with resultant effects on invertebrate colonization and population levels on snags (Marcy et al. 2005). In contrast, few fish species occur in high-elevation, cold-water streams, so predation pressure is exerted by fish assemblages with narrower dietary and behavioral breadth.

In our study, invertebrate densities were closely related to invertivore fish biomass, but not to total fish density or biomass. Relationships between invertebrate density and total fish abundance were obscured by highly variable data for fish feeding groups. For example, the percentages of total fish density and biomass composed of piscivores varied greatly from stream to stream and between the beginning and end of the experiment, ranging from 1.5 to 11% of fish

densities and from 6 to 77% of fish biomass (Table S1). If we excluded piscivores from our analyses, fish biomass estimates decreased by $\frac{1}{3}$ but density estimates remained essentially the same. When we focused only on the portion of the fish community potentially providing the strongest predation pressure on invertebrates, the invertivores, we detected fish effects on both colonizing and established communities (Fig. 3). The stronger invertivore effects on established than colonizing invertebrate abundances could have been related to the longer period of exposure of established communities to predators.

Fish predation reduced macroinvertebrate density, but fish had little effect on invertebrate biomass, perhaps because fish preyed more heavily on small than large individuals (similar to Worischka et al. 2015). This hypothesis was supported by our observation that the average size of individual macroinvertebrates in established communities increased with invertivore biomass (Fig. 4A). Many fish species occurring in these blackwater streams are small, have small mouths, and probably are gape limited. For example, *Notropis* spp. with small mouths were the most numerous drift feeders in this system (Marcy et al. 2005), and they may have reduced the immigration and emigration rates of small invertebrates to snags in enclosures, contributing to decreases in small invertebrate densities. Darters (*Etheostoma* spp.) are also small-mouthed diurnal invertivores (Marcy et al. 2005) that visually pick invertebrates from wood debris, stones, or vegetation (Roberts and Winn 1962, Orr and Resh 1989, Vogt and Coon 1990, Greenberg 1991). Juveniles of other invertivorous fish also were probably gape limited and preyed primarily on small prey. Dominant fish species, such as these, may have caused the reduced densities of invertebrates on snags when invertivore biomass was high. In contrast, madtoms (*Noturus* spp.) are nocturnal feeders that rely on taste rather than sight for prey detection (Jenkins and Burkhead 1993). Madtoms commonly feed on macroinvertebrate taxa that drift, but they mostly prey on benthic invertebrates, such as those at the edges of depositional zones where prey settle (Gutowski and Stauffer 1993, Burr and Stoeckel 1999). Thus, they would have little influence on snag communities.

In general, the predation effects we observed in these small blackwater systems could have been caused by simply sampling snags with low heterogeneity, the distance between available substrata, and the small mouth sizes of the most abundant invertivorous fishes. The effects could have been enhanced by increased predator efficiency and concentration on established snags.

Macroinvertebrate community

Immigration or prey replacement via drift is an important feature of most predation experiments in stream. Even when large-mesh fences are used, enclosures can become blocked by transported organic matter and effectively filter out any drifting macroinvertebrates. We removed accumu-

lated detritus from the upstream side of the fences daily and allowed the material to pass through the enclosures. Thus, we detected differences among our fish treatments even with relatively unrestricted immigration and colonization by drifting macroinvertebrates. The higher biomass and density of macroinvertebrates on established than on colonizing snags probably was a product of the increased duration of colonization, substratum conditioning, and biofilm development on established snags. However, high invertebrate densities on colonizing snags suggest that colonization is rapid on this limited substratum and underscores the importance of snag habitats in these productive systems.

We demonstrated that fish at high densities can significantly reduce invertebrate densities and alter invertebrate size structure in southeastern blackwater streams. The highly diverse and abundant stream fish faunas of the southeastern USA engender intense, size-selective predation on invertebrate communities, including both drifting and established prey, with snag communities being especially vulnerable. Despite the loss of statistical power subsequent to loss of 3 of the 5 streams in our original experimental design, we were able to document predator effects in the 2 remaining streams. These 2 streams appeared to be representative of other blackwater streams, but the generality of our results can be established only by conducting experiments in additional streams across the region.

Cyprinids and other small invertivores are dominant components of fish faunas in small streams throughout much of the eastern USA (Schlosser and Ebel 1989), but their influence on invertebrate community structure probably varies temporally and regionally. The strength of the effects of small invertivores can be modified by current velocity and algal biomass (Koetsier 1989, Schlosser and Ebel 1989). Other local factors could include the composition of predator and prey communities, substrata characteristics, habitat spatial heterogeneity, immigration and emigration rates, and stream productivity. Future investigators should examine the mechanisms by which fish predation modifies invertebrate trophic and community dynamics in low-gradient streams and how local stream conditions influence the effects of predators on their prey.

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Author contributions: JAL performed the field set up, collections, laboratory measurements, and preliminary statistics and prepared a rough draft of the manuscript. DEF provided expertise in fish identifications and fish ecology and assisted in the preparation of the manuscript. JVM provided guidance in selection of study question, experimental design, identification of invertebrates, statistics, and preparation of the manuscript. SDC contributed to manuscript revisions and editing.

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