HERPETOLOGICA

VOL. 77 JUNE 2021 NO. 2

Herpetologica, 77(2), 2021, 111–120
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Top-Down Effects of Salamanders on Macroinvertebrates in Fishless Headwater Streams

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Abstract: Salamanders are the top predators in many fishless headwater streams, and intraguild interactions among stream salamanders are well documented. However, little is known about the top-down effects of salamanders on stream food webs or how intraguild interactions mediate these effects. To investigate the effects of salamanders on macroinvertebrate communities of headwater streams, we conducted an experiment in stream mesocosms to test for effects of two stream salamander species, namely, *Eurycea bislineata* and *Gyrinophilus porphyriticus*, alone or in combination, on benthic and emerging macroinvertebrate density, biomass, and community composition. We also assessed intraguild interactions between these salamander species by comparing *Eurycea bislineata* survival and *G. porphyriticus* growth in single-species versus two-species treatments. *Gyrinophilus porphyriticus* reduced benthic macroinvertebrate densities when alone but not when co-occurring with *E. bislineata*. There were no effects of salamanders on benthic macroinvertebrate biomass or community composition and no effects on emerging macroinvertebrate density, biomass, or community composition. *Eurycea bislineata* survival decreased and *G. porphyriticus* weight increased in two-species treatments, suggesting that intraguild predation was occurring. Overall, although some of our findings are equivocal, these results suggest that salamanders can exert top-down control on macroinvertebrate communities in fishless headwater streams, decreasing benthic macroinvertebrate density. But this effect is dependent on the salamander species present, and can be removed by intraguild interactions between salamander species.

Key words: *Eurycea bislineata*; *Gyrinophilus porphyriticus*; Hubbard Brook Experimental Forest; Intraguild predation

Studies of aquatic food webs have produced many examples of top-down effects. The presence or absence of predators in freshwater and marine systems can have cascading effects that extend to the base of a food web (Power et al. 1985; Estes and Duggins 1995; Carpenter et al. 2001; Zimmer et al. 2001). In streams, these top predators are often fish, which have strong effects on benthic macroinvertebrates (Diehl 1992; Ruetz et al. 2002; Baxter et al. 2004; Winkelmann et al. 2014), as well as on macroinvertebrates emerging from streams (Baxter et al. 2004; Wesner 2010, 2016). By affecting emerging macroinvertebrates, fish regulate an important subsidy from streams to forests, where birds, spiders, bats, and lizards use emerging macroinvertebrates as a food source (Gray 1993; Sabo and Power 2002; Fukui et al. 2006; Marczak and Richardson 2007). But, many headwater streams are fishless (Richardson and Danehy 2007), and these streams account for 70% of total stream channel length in the United States alone (Leopold et al. 2012). By testing for top-down effects in fishless headwater streams, we can better understand the ecology of the headwater streams themselves, as well as riparian food webs.

In the absence of fish, salamanders are the top predators in many headwater streams of the eastern and western United States (Murphy and Hall 1981; Hawkins et al. 1983; Davic and Welsh 2004; Grant et al. 2009; Gould et al. 2017). These salamanders may co-occur with fish in the lower reaches of streams, but salamander populations often extend upstream of barriers that prevent fish colonization (Resetarits 1997; Lowe and Bolger 2002). Interactions among stream salamanders and between stream salamanders and fish have been the subject of classic studies in community ecology (Hairston 1987; Resetarits 1991, 1995). However, few studies have addressed the top-down effects of stream salamanders on other components of headwater communities, including—most obviously—macroinvertebrates. Reice and Edwards (1986) found no effect of *E. bislineata* on benthic macroinvertebrates, but that experiment lasted only 8 days and used adult *E. bislineata*, which are less likely than larvae to consume benthic macroinvertebrates (Burton 1976). Keitzer and Goforth (2013) found that *Eurycea wilderae* and *Desmognathus quadramaculatus* larvae decreased benthic macroinvertebrate abundances only when they co-occurred, but that experiment intentionally reduced the intraguild predation that normally occurs between *D. quadramaculatus* and *E. wilderae* by using individuals of similar size. It is possible that these salamanders would have had a different effect on benthic macroinvertebrates if intraguild predation was allowed to occur.

Benthic macroinvertebrates are known to be a significant component of the diet of larval and adult stream salamanders (Burton 1976; Lowe et al. 2005; Mondelli et al. 2014), and studies in pond and wetland systems show that salamanders can decrease benthic macroinvertebrate abundances (Blaustein et al. 1996; Benoy 2008; Reinhardt et al. 2017). A study by Progar and Moldenke (2002) found that temporary streams with neither fish nor salamanders produced a higher biomass of emerging macroinvertebrates than perennial

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streams, which were assumed to have salamanders and/or fish. Also, Atlas and Palen (2014) used a model to show that salamander predation can reduce benthic and emerging macroinvertebrate biomass, both when salamanders occur alone and when they co-occur with fish. These studies suggest that salamanders may exert top-down pressure on benthic and emerging macroinvertebrates, with implications for both stream and forest ecosystems. Furthermore, because multiple salamander species often co-occur in streams, with a wide range of resulting intraguild interactions (Hairston 1980; Gustafson 1993; Jaeger et al. 1998; Bruce 2008), any assessment of top-down effects on macroinvertebrates must account for these intraguild interactions.

From work in other systems, we know that intraguild interactions among predators can determine effects on shared prey. For example, when intraguild competition results in predators using different habitats, this can reduce spatial refugia for shared prey (Van Son and Thiel 2006; Steinmetz et al. 2008). The resulting decrease in prey survival is known as risk enhancement (Sih et al. 1998). Alternatively, intraguild predation or interference competition can increase survival rates of shared prey (Soluk and Collins 1988; Fauth 1990; Vance-Chalcraft and Soluk 2005), a result known as risk reduction (Sih et al. 1998). For example, under intraguild predation, the consumption of one predator (i.e., the intraguild prey) by the other predator (i.e., the intraguild predator) releases the shared prey from top-down control by the intraguild prey species (Polis et al. 1989). Many studies have documented intraguild predation in stream salamander communities (Gustafson 1993; Bruce 2008; Vance-Chalcraft et al. 2007), suggesting that top-down effects of stream salamanders on benthic macroinvertebrates may be altered by interactions between co-occurring salamander species.

The salamanders *G. porphyriticus* and *E. bislineata* are common throughout the headwater streams of New Hampshire, USA, occurring both together and alone (Burton and Likens 1975; Barr and Babbitt 2002; Lowe and Bolger 2002; Lowe 2005; Lowe et al. 2012). Both species are confined to the stream channel as larvae. *Gyrinophilus porphyriticus* has a larval period of 3–5 yr and *E. bislineata* has a larval period of 1–2 yr (Bruce 1980, 1985). Adult *G. porphyriticus* may remain in the stream channel or forage in the riparian forest at night, but are found under rocks and wood in and along the stream channel during the day (Greene et al. 2008). Adult *E. bislineata* may move over 100 m into the forest after metamorphosis and return to the stream to breed (MacCulloch and Bider 1975; Petranka 1998). In New Hampshire, larvae of both species feed primarily on aquatic macroinvertebrate larvae in the benthos (Burton 1976). The occasional presence of terrestrial macroinvertebrates and winged aquatic macroinvertebrate adults in larval diets suggests that both species also feed at the water's surface (Burton 1976; Lowe et al. 2005).

Gyrinophilus porphyriticus and *E. bislineata* exhibit intraguild predation when they co-occur; larvae and adults of the much smaller *E. bislineata*, the intraguild prey, are consumed by larvae and adults of *G. porphyriticus*, the intraguild predator (Burton 1976; Petranka 1998; Lowe et al. 2005). In mesocosm experiments, Resetarits (1991) found that *E. bislineata* larvae experienced reduced growth rates in the presence of *G. porphyriticus* larvae, presumably due to altered foraging behavior of the prey. Larvae of *Eurycea cirrigera*, a closely related species to *E. bislineata*, also showed reduced nocturnal foraging and decreased survival in the presence of *G. porphyriticus* larvae (Gustafson 1993; Rudolf 2006).

Here, our goal was to advance understanding of the role of stream salamanders in headwater food webs by testing for individual and combined effects of *G. porphyriticus* and *E. bislineata* on benthic and emerging macroinvertebrates, while explicitly incorporating intraguild interactions. Specifically, we used a stream mesocosm experiment to test the following predictions: (1) *G. porphyriticus* and *E. bislineata* will each reduce benthic macroinvertebrate densities and biomass and alter community composition through direct, top-down effects; (2) these direct effects will carry over to emerging macroinvertebrates; and (3) intraguild interactions between *G. porphyriticus* and *E. bislineata* will alter their effects on shared macroinvertebrate prey. If prediction (1) was supported, it would indicate that macroinvertebrate communities in fishless headwater streams experience top-down control when salamanders are present, with potential implications for basal components of headwater food webs (e.g., algae, leaf litter; Power 1990; Townsend 2003; Baxter et al. 2004; Woodward et al. 2008) and associated ecosystem processes (e.g., productivity and nutrient retention; Baxter et al. 2005; Eby et al. 2006). If prediction (2) was supported, it would mean that salamanders affect the flow of macroinvertebrate subsidies from streams to forests, thereby potentially affecting terrestrial food webs (Gray 1993; Nakano and Murakami 2001; Sabo and Power 2002; Fukui et al. 2006). Finally, if prediction (3) were supported, it would indicate that the specific salamander assemblage in a stream determines top-down effects on aquatic macroinvertebrates, as well as resulting subsidies and ecosystem processes. Importantly, support for prediction (3) would help connect the influential body of work on stream salamander community ecology (Hairston 1980; Gustafson 1993; Jaeger et al. 1998; Bruce 2008) to the equally influential body of work on headwater ecosystem ecology (Fisher and Likens 1973; Wallace et al. 1997; Townsend et al. 1997; Gulis and Suberkropp 2003).

Materials and Methods

Study Site

This experiment was conducted within the Hubbard Brook Experimental Forest (HBEF) in the White Mountains Region of central New Hampshire. There are many small, fishless headwater streams within the 31.6-km^2 area of the HBEF (Warren et al. 2008). These streams tend to be slightly acidic (pH ≈ 5.48), with high dissolved oxygen (80–90%), mild midday summer temperatures (13.0–17.0°C), a base flow rate of 1 L s^{-1}, and low conductivity (mean = 17.4 μS cm^{-1}; Likens and Buso 2006; Likens 2013). The HBEF streams also tend to be heterotrophic and nutrient poor, with primary productivity contributing less than 1% of energy and most carbon entering the system through allochthonous inputs (Fisher and Likens 1973; Mayer and Likens 1987).

Experimental Design

We used stream mesocosms to test how stream salamanders affect benthic and emerging macroinvertebrate density,

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biomass, and community composition. The salamander treatment had the following four levels: *E. bislineata* alone (EBIS), *G. porphyriticus* alone (GPOR), *E. bislineata* and *G. porphyriticus* (BOTH), and no-salamander controls (CONTROL). Comparing EBIS and GPOR to CONTROL allowed us to assess the effects of these salamander species individually on benthic and emerging macroinvertebrates. The BOTH treatment allowed us to assess how salamander intraguild interactions affect benthic and emerging macroinvertebrates. Each of these treatments was replicated 4 times for a total of 16 mesocosms.

Experimental mesocosms were 189-L polyethylene tubs set along the bank of Zig-Zag Brook in the HBEF and modeled after of those of Davenport and Lowe (2015). Mesocosms were 1 m long, 0.54 m wide, and 0.46 m high with a water depth of 0.19 m. Mesocosm substrates were composed of materials approximating those of streams at the HBEF by using a similar approach to Resetarits (1991). Each mesocosm contained 7 L of untreated playground sand, 7 L of pea gravel, 8 L of gravel, 7 small cobble stones measuring 8–10 cm in diameter, and 3 large cobble stones measuring 15–34 cm in diameter. Each mesocosm also received 600 mL of leaf litter gathered from along the bank of Zig-Zag Brook. To prevent salamanders from climbing out of mesocosms, an overhang of aluminum was affixed to the rim of each mesocosm with silicone sealant and coated with petroleum jelly. This overhang extended 5.5 cm over the water, bent downward at a right angle, and continued 7.5 cm. A 1-cm-wide line of petroleum jelly coated the terminal portion of each overhang.

Water was gravity fed to each mesocosm through two arrays of pipes running from Zig-Zag Brook. To prevent bias in the distribution of water among mesocosms, each array delivered water to eight mesocosms and split in a symmetrical branching pattern, forming a balanced binary tree. An adjustable valve on the inflow of each mesocosm allowed us to maintain a flow rate of 2.4 L min^{-1}. Flow rate was measured twice weekly and adjusted as needed. Water exited the mesocosms through screens with a mesh size of 0.02 cm^2. The intake for each of the two arrays of pipes was covered with a PVC filter and a bag with mesh size of 0.2 cm^2. This intake was intended to prevent leaf litter, salamanders, and macroinvertebrates from entering the mesocosms, while also maintaining water flow from the stream. The intakes were submerged in a deep pool upstream of the mesocosms.

We collected benthic macroinvertebrates for the mesocosms from Zig-Zag Brook on 25 June and 30 June 2014. We had to spread our collection over multiple days due to time constraints and a high flow event in the collection stream. Each mesocosm received benthic macroinvertebrates from separate 0.6-m^2 quadrats of run habitat in Zig-Zag Brook. During collection, the top inch of stream substrate was disturbed by hand for 4 min and by kicking for 1 min in front of a D-frame net of mesh size 800 × 900 μm. Then, to assess initial benthic macroinvertebrate density, biomass, and community composition, we placed one Hester-Dendy sampler (NKY Environmental Supply) into each mesocosm on 30 June 2014 and left them in place for 2 wk before adding salamanders. Hester-Dendy samplers have been used to sample benthic macroinvertebrates from mesocosms (King and Richardson 2003; Kaatz et al. 2010) and experimental enclosures (Brazner and Kline 1990). Hester-Dendy samplers were selected for this experiment because they do not disturb the substrate of the mesocosms (Hester and Dendy 1962). A single Hester-Dendy sampler consisted of a stack of eight square plates of tempered hardboard attached to each other by a bolt through a hole at the center of each plate. Washers maintain space between the plates for macroinvertebrates to colonize. Each plate was 7.62 cm × 7.62 cm, and the total sampling area was 774.2 cm^2.

After calculating the initial density of benthic macroinvertebrates in each mesocosm, we created the following four blocks representing categories of initial density: low (13–142 individuals m^{-2}), mid-low (220–245 individuals m^{-2}), mid-high (245–271 individuals m^{-2}), and high (323–491 individuals m^{-2}). Variation in initial prey densities can alter multipredator effects (Peckarsky 1991; Griffen 2006), and blocking allowed us to account for this variation in our analyses (Zar 1996). Salamander treatments were assigned to the four blocks by using a randomized complete block design. All salamanders were collected from Bagley Trail Brook in the HBEF and randomly assigned to a treatment and mesocosm. Salamanders were added to their assigned mesocosm on 22 July 2014. Like natural streams, mesocosms were open to colonization by flying aquatic insects and inputs of falling leaf litter and terrestrial insects. The experiment ran for 51 d.

We used a biomass-based substitutive experimental design to assess the effects of salamander treatments on macroinvertebrate prey (Siddon and Witman 2004; Griffen 2006; Carey and Wahl 2010). This method allowed us to accommodate the large size difference between *E. bislineata* larvae (mean wet mass ± 1 SE = 0.21 ± 0.003 g) and *G. porphyriticus* larvae (mean wet mass ± 1 SE = 1.97 ± 0.10 g). Alternative designs frequently use one individual of each predator species in multipredator treatments (Siddon and Witman 2004; Vance-Chalcraft et al. 2004; Griffen 2006), keeping the density of predators constant across single- and multipredator treatments. However, this would have resulted in unrealistically low *E. bislineata* densities for our system (i.e., 1.85–3.70 individuals m^{-2}).

To hold salamander biomass constant across treatments, we considered eight *E. bislineata* larvae to be roughly equivalent to one *G. porphyriticus* larva (please see wet masses, above). Therefore, the EBIS treatment consisted of 16 larval *E. bislineata*, resulting in a density of 29.6 individuals m^{-2}. The GPOR treatment consisted of 2 larval *G. porphyriticus*, resulting in a density of 3.4 individuals m^{-2}. The BOTH treatment consisted of 1 *G. porphyriticus* and 8 *E. bislineata*, with a density of 1.9 individuals m^{-2} and 14.8 individuals m^{-2}, respectively. Total salamander biomass across treatments ranged from 3.22 to 4.83 g (mean ± 1 SE = 3.75 ± 0.14 g). Salamander treatment densities were conservative but within the range of natural densities reported for *G. porphyriticus* (0.16–10 individuals m^{-2}) and *E. cirrigera* (23–169 individuals m^{-2}), a sister taxon of *E. bislineata* (Resetarits 1991; Nowakowski and Maerz 2009; Davenport and Lowe 2016).

Eleven *E. bislineata* larvae of a smaller size class than that used in experimental treatments (i.e., obviously shorter snout–vent length [SVL]) were retrieved from the mesocosms at the end of the experiment. Specifically, the *E. bislineata* that entered the mesocosms were ≤1.4 cm in SVL,

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whereas the experimental animals were ≥2.0 cm SVL. Two of these *E. bislineata* were removed from EBIS mesocosms, three from GPOR mesocosms, two from BOTH mesocosms, and four from CONTROL mesocosms. We assume that these *E. bislineata* entered the mesocosms through the array of pipes delivering stream water, with their small size allowing them to bypass the PVC and mesh filters on the intake valves. In the Discussion, we address how these immigrants—or possible emigration of *E. bislineata* individuals—may have influenced our results. Because of the limited degrees of freedom in our experimental design, simply excluding mesocosms with immigrants from analyses was not possible. Direct comparisons of response variables in mesocosms with and without immigrants were nonsignificant ($P > 0.05$), but these results are not surprising considering the small number and size of immigrants. All *G. porphyriticus* individuals added to mesocosms were recovered at the end of the experiment, and no additional *G. porphyriticus* individuals were found in mesocosms.

Benthic Macroinvertebrates

To test for effects of salamander treatments on benthic macroinvertebrates, Hester-Dendy samplers were added to each mesocosm on 18 August 2014 and left in place for 2 wk (Hester and Dendy 1962; Dudgeon 1996). The Hester-Dendy plates were spaced sufficiently far apart to allow salamanders of both species to access benthic macroinvertebrates. Hester-Dendy samplers were removed on 2 September 2014, during the last week of the experiment, when benthic macroinvertebrate communities had been exposed to salamander treatments for 6 wk. Benthic macroinvertebrates were stored in 75% ethanol for identification.

Benthic macroinvertebrates were identified to the level of family for insects and subclass for all other macroinvertebrates (Merrit and Cummins 1996; Voshell 2002). We expected family to be a sufficient taxonomic resolution for this study due to the strong correlation between species and family diversity (Heino and Soininen 2007). Storage of samples in ethanol dehydrates the organisms and leads to a varying loss of dry weight (Leuven et al. 1985; Wetzel et al. 2005; Edwards et al. 2009). Therefore, to avoid error introduced by the storage of our samples in ethanol, we calculated biomass by using published length–mass relationships at the level of order, or suborder for Diptera (Benke et al. 1999). Macroinvertebrate lengths were measured using a stereoscopic microscope with an ocular micrometer. The biomass of benthic macroinvertebrates in the EBIS treatment could only be calculated for three replicates because the single individual found in one replicate was damaged during processing, preventing us from measuring its length accurately.

Emerging Macroinvertebrates

Emerging macroinvertebrates were sampled over 72 h by using mesh nets suspended above the mesocosms and connected to collection jars (Wesner 2010; Merten et al. 2014). Nets were fastened along the top of mesocosms to prevent emerging macroinvertebrates from escaping. Collection took place from 3 September 2014 to 6 September 2014, during the last week of the experiment, when benthic macroinvertebrate communities had been exposed to salamander treatments for 6 wk. Macroinvertebrates were removed from collection jars and placed in 75% ethanol. Each net had a skirt with a mesh size of 750 μm^2 and an upper portion of net with mesh size of 1.1 mm × 1.7 mm. Nets were connected to a collection jar with an inverted funnel of opening size 10 cm. Emerging macroinvertebrates were killed using a 2.5-cm^2 section of commercially available insect poison hung inside each jar (Prozap Insect Guard, Chem-Tech Ltd). Emerging macroinvertebrates were identified to family, except when prohibited due to damage (Merrit and Cummins 1996). To avoid error introduced by the storage of our samples in ethanol, we calculated biomass using published length–mass relationships at the level of order or suborder (Sabo et al. 2002). Macroinvertebrate lengths were measured using a stereoscopic microscope with an ocular micrometer.

Salamander Survival and Growth

We compared the survival of *E. bislineata* in treatments with just *E. bislineata* (EBIS) and with *G. porphyriticus* (BOTH) to determine if intraguild predation occurred between these two species. Survival was quantified as the proportional change in abundance ([final abundance/initial abundance] − 1), for which the initial abundance was the number of *E. bislineata* originally added to a mesocosm on 22 July 2014 and final abundance was the number of these experimental animals remaining in that mesocosm on 11 September 2014. The small size of the *E. bislineata* immigrants allowed us to remove them from these estimates of *E. bislineata* survival.

We measured the proportional change in mass of *G. porphyriticus* individuals ([final mass/initial mass] − 1) in treatments with and without *E. bislineata* (BOTH versus GPOR) to further assess if intraguild predation was occurring. If intraguild predation occurred, we expected *G. porphyriticus* individuals to gain more mass in the BOTH treatments than in the GPOR treatments, in which the only prey resource was benthic macroinvertebrates (Holt and Polis 1997). To quantify change in mass, each *G. porphyriticus* was weighed before addition to mesocosms and at the end of the experiment. To track weight changes, all *G. porphyriticus* individuals were separately marked using a florescent visible implant elastomer tag injected subcutaneously in the dorsal region (Northwest Marine Technology, Inc.).

Statistical Analyses

To test for an effect of salamander treatment on final benthic macroinvertebrate density and biomass, we used an analysis of variance (ANOVA). Specifically, we used a randomized complete block design and blocked by our four levels of initial benthic macroinvertebrate density. Final benthic macroinvertebrate density was calculated by dividing the total number of individuals collected from each Hester-Dendy sampler by the surface area of the sampler (774.2 cm^2). Densities were square-root transformed to meet the assumptions of ANOVA. We used the same methods to test for an effect of salamander treatment on final benthic macroinvertebrate biomass, also with initial benthic macroinvertebrate densities as our blocking factor. If a significant effect of salamander treatment was found, we assessed multipredator effects using a two-tailed paired sample *t*-test

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to compare expected and observed benthic macroinvertebrate density at each level of initial benthic macroinvertebrate density (Schmitz and Sokol-Hessner 2002; Siddon and Witman 2004). Predicted predator effects in the BOTH treatment were calculated using the equation $P_{BOTH} = (O_{EBIS} + O_{GPOR})^{0.5}$, where O_{EBIS} is the observed predator effect in the EBIS treatment, O_{GPOR} is the observed predator effect in the GPOR treatment, and P_{BOTH} is the predicted multipredator effect in the BOTH treatment (Griffen 2006; Carey and Wahl 2010).

To test how stream salamanders affected benthic macroinvertebrate taxonomic richness and diversity, we used both taxonomic richness (S) and the exponential of the Shannon–Wiener Index (Exp H') as response variables. These indices are widely used, statistically robust, and biologically relevant (Gray 2000; Hubálek 2000; Jost 2007). We excluded macroinvertebrates that were too damaged to be identified to the level of family (for insects) or subclass (for oligochaetes) from these analyses. Again, we compared results across salamander treatments by using a randomized complete block design ANOVA and blocking by initial benthic macroinvertebrate density. The Exp H' of the GPOR treatment could only be calculated for two replicates out of four because there were no benthic macroinvertebrates on the samplers collected from two of the GPOR treatments.

To test for an effect of salamander treatment on emerging macroinvertebrate density, biomass, and taxonomic diversity, we used the same ANOVA structure described above. The density of emerging macroinvertebrates per square meter per day was obtained by dividing the number of emerging macroinvertebrates by the surface area of the mesocosm (0.54 m^2) and the number of days the emergence traps were up (3 d). The biomass of emerging macroinvertebrates was also expressed as m^{-2} d^{-1}, and we used S and Exp H' to test how stream salamanders affected emerging macroinvertebrate taxonomic diversity.

To visualize differences in community composition of benthic and emergent macroinvertebrates among salamander treatments, we created nonmetric multidimensional scaling (NMDS) plots with the metaMDS function in the R package vegan (Oksanen et al. 2019). To test for differences in community composition among salamander treatments, we ran a permutation multivariate analysis of variance (PERMANOVA) using the adonis function in vegan (Oksanen et al. 2019). We used the Bray–Curtis dissimilarity matrix with 999 permutations.

It is possible that sampled benthic and emerging macroinvertebrates did not represent the same communities due to macroinvertebrate phenology (Merrit and Cummins 1996; Progar and Moldenke 2002; Macneale et al. 2005) or differences in sampling methods (Malison et al. 2010). The emergence of macroinvertebrates from streams is not constant, as different taxa emerge at different times (Merrit and Cummins 1996; Progar and Moldenke 2002; Baxter et al. 2005). In contrast, the benthic macroinvertebrate community is more consistent and represents a broader range of taxa at any given time (Mackay and Kalff 1969; Merrit and Cummins 1996; Macneale et al. 2005). To assess the correspondence of the benthic and emerging macroinvertebrate communities at the time of sampling, we ran a PERMANOVA on the CONTROL treatments. Only the CONTROL treatments were used for the PERMANOVA to ensure that any differences between benthic and emerging macroinvertebrate communities were due to macroinvertebrate phenology or sampling methods and not predation by salamanders. Again, we used the adonis function in vegan and a Bray–Curtis dissimilarity matrix with 999 permutations (Oksanen et al. 2019).

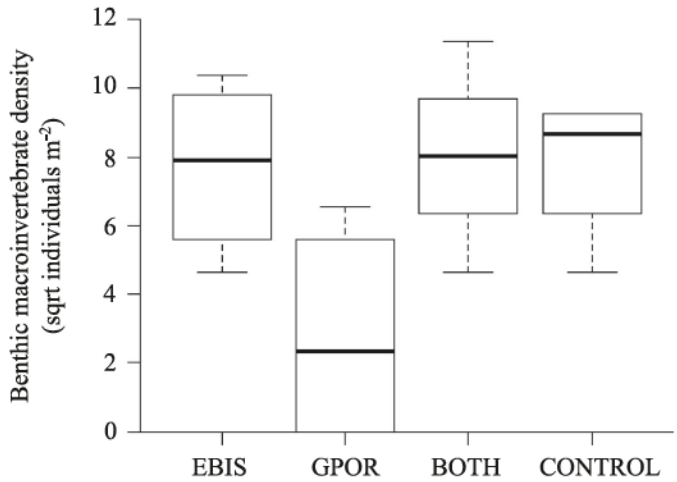

FIG. 1.—Box plot of benthic macroinvertebrate densities in mesocosms with treatments consisting of *Eurycea bislineata* alone (EBIS), *Gyrinophilus porphyriticus* alone (GPOR), *E. bislineata* and *G. porphyriticus* (BOTH), and no-salamander controls (CONTROL). Experimental mesocosms were placed along Zig-Zag Brook at the Hubbard Brook Experimental Forest, NH, USA. There were four replicate mesocosms per treatment. The experiment ran from 22 July to 10 September 2014. Box plots show median and interquartile range, and whiskers show minimum and maximum values. When a whisker is not present, it indicates that the minimum or maximum value is equivalent to the upper or lower quartile.

To analyze the proportional survival of *E. bislineata* in EBIS versus BOTH treatments, we used a one-tailed Mann–Whitney–Wilcoxon test due to lack of normality. We used a one-tailed test based on the a priori expectation that *G. porphyriticus* would reduce the survival of *E. bislineata* (Burton 1976; Lowe et al. 2005). We used a two-tailed student's *t*-test to analyze the proportional weight change of *G. porphyriticus* in GPOR versus BOTH treatments. Although we expected the intraguild prey's presence to benefit the intraguild predator, this test was two tailed because Gustafson (1993) found that the availability of *E. cirrigera* larvae, a sister species of *E. bislineata*, did not increase larval *G. porphyriticus* growth rates. Each of the two *G. porphyriticus* individuals in GPOR mesocosms were treated as independent replicates for this analysis, but we also tested for an effect by using average weight change for the two individuals in GPOR mesocosms. All statistical analyses were conducted in R v3.1.1 (R Core Development Team 2017).

RESULTS

Benthic Macroinvertebrates

There was a significant effect of salamander treatment on benthic macroinvertebrate densities ($F_{3,9} = 4.05$, $P = 0.04$; Fig. 1), and a significant nonadditive multipredator effect ($t_3 = -4.32$, $P = 0.02$, two-tailed test). Specifically, mean benthic macroinvertebrate density was significantly lower in the GPOR treatment than in the remaining treatments, which were remarkably similar (Table 1). In treatments with both *G. porphyriticus* and *E. bislineata*, there was no

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TABLE 1.—Summary of density, biomass, taxonomic richness (S), and exponential of the Shannon–Wiener Index (Exp H') by treatment for benthic and emergent macroinvertebrates in stream mesocosms. Values are means ± SE. Salamander treatments had four levels, as follows: *Eurycea bislineata* alone (EBIS), *Gyrinophilus porphyriticus* alone (GPOR), *E. bislineata* and *G. porphyriticus* (BOTH), and no-salamander controls (CONTROL). Each treatment was replicated four times; however, the biomass of benthic macroinvertebrates in the EBIS treatment could only be calculated for three replicates. The Exp H' of the GPOR treatment could only be calculated for two replicates out of four because there were no benthic macroinvertebrates on the samplers collected from two of the GPOR treatments.

	Benthic macroinvertebrates				Emergent macroinvertebrates			
Treatment	Density (ind. m^{-2})	Biomass (mg. m^{-2})	S	Exp H'	Density (ind. $m^{-2}d^{-1}$)	Biomass (mg $m^{-2}d^{-1}$)	S	Exp H'
EBIS	39 ± 12	4 ± 2	1.75 ± 0.48	1.57 ± 0.34	10 ± 2	4 ± 1	2.25 ± 0.25	1.63 ± 0.14
GPOR	10 ± 6	9 ± 8	0.5 ± 0.29	1 ± 0	20 ± 5	7 ± 2	2.50 ± 0.50	1.33 ± 0.13
BOTH	42 ± 13	59 ± 39	1.75 ± 0.48	1.69 ± 0.45	19 ± 3	7 ± 1	2.25 ± 0.25	1.36 ± 0.15
CONTROL	39 ± 9	20 ± 6	2 ± 0.41	1.78 ± 0.39	21 ± 6	8 ± 2	3.25 ± 0.48	1.53 ± 0.14

reduction in macroinvertebrate density relative to the control treatment. Salamander treatment did not affect benthic macroinvertebrate biomass ($F_{3,9} = 1.70$, $P = 0.24$), taxonomic richness ($F_{3,9} = 3.3$, $P = 0.07$), or species diversity ($F_{3,7} = 0.59$ $P = 0.64$). Block effects were not significant in these ANOVAs ($P > 0.05$). Community composition did not differ among salamander treatments (PERMANOVA, $F' = 0.32$, $P = 0.97$; Fig. 2). The abundance of benthic macroinvertebrate taxa by treatment is given in Supplemental Table S1 (available online).

Emerging Macroinvertebrates

Salamander treatment did not affect the densities of emerging macroinvertebrates ($F_{3,9} = 1.11$, $P = 0.40$) or the biomass of emerging macroinvertebrates ($F_{3,9} = 1.19$, $P = 0.37$). There was also no effect of salamander treatment on the taxonomic richness ($F_{3,9} = 1.23$, $P = 0.35$) or species diversity ($F_{3,9} = 1.14$, $P = 0.38$) of emerging macroinvertebrates. Block effects were not significant in these ANOVAs ($P > 0.05$). Community composition did not differ among salamander treatments (PERMANOVA, $F' = 1.49$, $P = 0.25$; Fig. 2). The abundance of emerging macroinvertebrate taxa by treatment is given in Supplemental Table S2 (available online).

Community Dissimilarity

Benthic and emerging macroinvertebrate communities in CONTROL treatments were significantly different (PERMANOVA, $F' = 7.78$, $P = 0.04$). This result indicates that emerging macroinvertebrates represent a subset of the benthic macroinvertebrate community present in each mesocosm and justified separate analyses of the benthic and emerging macroinvertebrate data.

Salamander Survival and Growth

Survival of *E. bislineata* was higher in the EBIS treatment than in the BOTH treatment, indicating that the presence of *G. porphyriticus* reduced the survival of *E. bislineata* (W = 16, $P = 0.01$, one-tailed test; Fig. 3A). *G. porphyriticus*

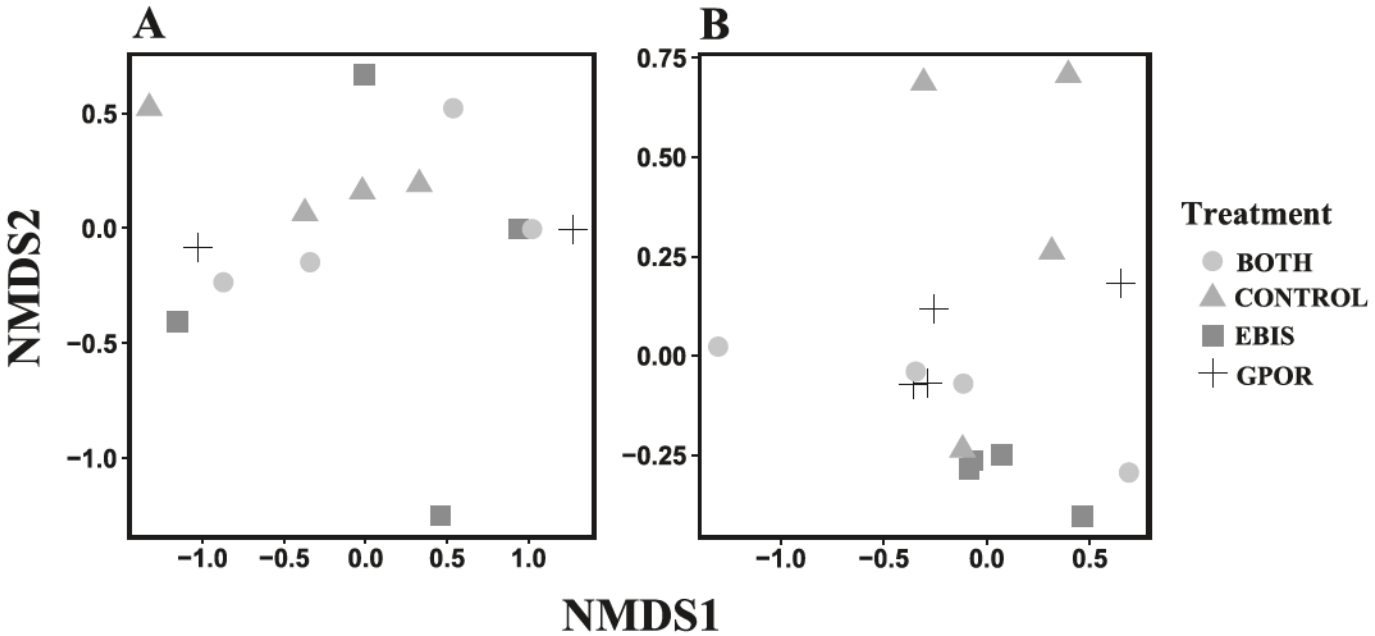

FIG. 2.—Nonmetric multidimensional (NMDS) ordination of benthic (A) and emergent (B) macroinvertebrate communities (stress = 0.04 and 0.08, respectively) across the four salamander treatments (BOTH = *Eurycea bislineata* and *Gyrinophilus porphyriticus*, CONTROL = no-salamander controls, EBIS = *E. bislineata* alone, and GPOR = *G. porphyriticus* alone). Each point represents the community composition of invertebrates in a single mesocosm; points that are closer together have more similar communities than points that are more distant. There were four replicate mesocosms per treatment, but benthic macroinvertebrate counts were zero in two GPOR mesocosms (Supplemental Table S1, available online), so there are two points for that treatment in the left figure.

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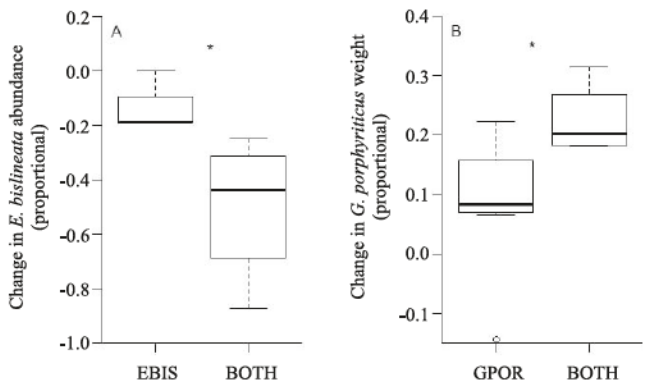

Fig. 3.—Box plots of proportional *Eurycea bislineata* survival (A) and change in *Gyrinophilus porphyriticus* weight (B) by salamander treatment. Experimental mesocosms were placed along Zig-Zag Brook at the Hubbard Brook Experimental Forest, NH, USA. The experiment ran from 22 July to 10 September 2014. Treatments were *E. bislineata* alone (EBIS), *G. porphyriticus* alone (GPOR), and *E. bislineata* and *G. porphyriticus* (BOTH). There were four replicate mesocosms per treatment. For the analysis of change in weight, *G. porphyriticus* individuals were treated as independent replicates (GPOR: $n = 8$, BOTH: $n = 4$). Asterisks indicate significant differences between treatment levels at $P < 0.05$. Box plots show median and interquartile range, and whiskers show minimum and maximum values, excluding outliers, which are shown as open circles. When a whisker is not present, it indicates that the minimum or maximum value is equivalent to the upper or lower quartile.

individuals also gained proportionally more weight in the BOTH treatment than the GPOR treatment ($t_{10} = -2.29$, $P = 0.04$, two-tailed test; Fig. 3B). This test was also significant after removing the outlier *G. porphyriticus* individual indicated in Fig. 3B ($t_9 = -2.67$, $P = 0.03$) and when we use average weight change for the two individuals in GPOR mesocosms rather than treating each individual as an independent observation ($t_6 = -2.54$, $P = 0.04$). These results further suggest that *G. porphyriticus* preyed on *E. bislineata* individuals.

Discussion

Benthic macroinvertebrate densities were significantly reduced in GPOR treatments relative to all other treatments, despite the low (but realistic) densities of *G. porphyriticus* larvae applied (3.4 individuals m^{-2}; Resetarits 1991; Davenport and Lowe 2016). Fish are known to decrease the densities of both benthic and emerging macroinvertebrates (Baxter et al. 2004; Wesner 2010, 2013), but until now there was little evidence that salamanders could also have this effect (but see Keitzer and Goforth 2013). More broadly, our findings indicate that benthic macroinvertebrate communities may experience top-down regulation by predators even in fishless headwater streams (Wipfli and Gregovich 2002; Richardson and Danehy 2007).

The negative effect of *G. porphyriticus* on benthic macroinvertebrate densities was removed when its intraguild prey *E. bislineata* was present. This finding suggests that the specific composition of the stream salamander community can influence the abundance of shared macroinvertebrate prey and the top-down regulation experienced by these prey. When *G. porphyriticus* and *E. bislineata* were together in mesocosms, *G. porphyriticus* individuals gained more weight and *E. bislineata* experienced reduced survival than when each species occurred alone (Fig. 3). These results are consistent with our hypothesis that intraguild predation between *G. porphyriticus* and *E. bislineata* would occur and also match a previous study in which larval *G. porphyriticus* growth increased and survival of their intraguild prey (*E. wilderae*) decreased when they co-occurred (Beachy 1994).

Intraguild predation by *G. porphyriticus* on *E. bislineata* resulted in risk reduction for the salamanders' shared benthic macroinvertebrate prey—the expected outcome when predators interfere with each other (Sih et al. 1998). This finding adds to a body of research showing that intraguild predation results in risk reduction for shared prey (Huang and Sih 1991; Crumrine and Crowley 2003; Griffen and Byers 2006). These results contrast with results showing that stream salamanders decreased benthic macroinvertebrate abundance when two species (*D. quadramaculatus* and *E. wilderae*) were present (Keitzer and Goforth 2013). However, Keitzer and Goforth (2013) sought to limit intraguild predation by using only small *D. quadramaculatus* individuals, which reduced the size difference between the two salamander species. This reduction in size variation and the resulting decrease in the intensity of intraguild interactions may have led to the observed risk enhancement in the shared macroinvertebrate prey. More generally, the combination of results from our experiment and Keitzer and Goforth (2013) reinforce a broader conclusion that the composition of the stream salamander community—specifically interactions among salamander species—influences the strength of top-down effects on stream macroinvertebrates.

A known pitfall of substitutive designs, including the biomass-based modification used here, is that they confound a decrease in intraspecific interactions with an increase in interspecific interactions. Specifically, in our design, the BOTH treatment had half the number of *G. porphyriticus* individuals as the GPOR treatment. However, additive designs, the common alternative to substitutive designs, confound changes in predator density with changes in predator diversity (Sih et al. 1998; Griffen 2006; Schmitz 2007). We were unable to run both additive and substitutive designs concurrently due to the limited number of stream mesocosms we could create and maintain. Therefore, we cannot fully separate the effects of decreasing *G. porphyriticus* density from the effects of intraguild predation between *G. porphyriticus* and *E. bislineata*. It is possible, then, that release from intraspecific interactions contributed to the increase in *G. porphyriticus* weight in the BOTH versus the GPOR treatment. It seems unlikely, however, that these intraspecific interactions explain the reduction in *E. bislineata* survival in the BOTH treatment (Fig. 3A) or the similarity of benthic macroinvertebrate densities in BOTH and CONTROL mesocosms relative to GPOR (Fig. 1).

In addition to showing the top-down implications of intraguild predation, our findings suggest that the roles of salamanders in stream food webs likely differ among species. Unlike *G. porphyriticus*, larval *E. bislineata* did not affect benthic macroinvertebrate densities when they occurred alone. Benthic macroinvertebrate densities in mesocosms with only *E. bislineata* were not significantly different from densities in predator-free control mesocosms. This result is consistent with a previous study showing that adult *E. bislineata* did not affect benthic macroinvertebrate prey (Reice and Edwards 1986). These results suggest that in streams with only *E. bislineata*, benthic macroinvertebrates

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are likely regulated primarily by bottom-up, instead of top down, mechanisms (Johnson and Wallace 2005).

It is important to acknowledge that several small *E. bislineata* larvae gained access to the mesocosms in some way. We believe it is unlikely that these immigrants altered the main findings of the experiment for the following 3 reasons: (1) *E. bislineata* treatments (16 individuals per mesocosm) did not affect benthic macroinvertebrate densities (EBIS in Fig. 1), so immigrants cannot account for the reduction in benthic macroinvertebrate densities in GPOR mesocosms; (2) the small size of immigrants allowed us to exclude them from calculations of *E. bislineata* survival, and the possibility that immigrants were eaten by *G. porphyriticus* in BOTH mesocosms does not invalidate the reduced survival of experimental animals (Fig. 3A); and (3) only 4 immigrants were found in CONTROL mesocosms where there was no possibility of predation, suggesting that the rate of immigration was very low. We believe it is very unlikely that our focal *E. bislineata* larvae escaped from the mesocosms because of the small mesh size on the exit drains (0.02 cm^2) and aluminum overhangs coated with petroleum jelly. Additionally, the spigots delivering water to the mesocosms were suspended approximately 20 cm above the surface of the water, fed by hoses that extended out from the mesocosm walls by 10–15 cm. It would be very difficult for a larva to navigate those barriers—in addition to the incoming water velocity—to escape through the inflow pipes.

The effects of multiple predators on shared prey can depend on initial prey density (Peckarsky 1991; Griffen 2006); yet, it is often difficult to assess and control for variation in macroinvertebrate prey densities in field mesocosms. By seeding the mesocosms with benthic macroinvertebrates 2 wk before the addition of salamanders, we were able to measure benthic macroinvertebrate density in each mesocosm just before salamander addition and block based on initial density. Salamander treatments were then assigned randomly to mesocosms in each of these blocks. Considering the variation in initial macroinvertebrate densities among and within these blocks (e.g., low-density mesocosms had 13–142 individuals m^{-2}), we are confident that the effect of *G. porphyriticus* (Fig. 1) is relevant to natural stream systems, where macroinvertebrate densities vary at fine spatial scales (Downs et al. 1995). Nevertheless, maintaining water flow in field-based stream mesocosms brings the possibility of ongoing colonization. To limit colonization, we placed a PVC filter and mesh bag (0.2-cm^2 mesh size) around the inflow valves of the water pipes. Despite these efforts, the input of several small *E. bislineata* larvae suggests that these systems were not entirely closed to colonization. However, any additional—although unbiased—variation in macroinvertebrate densities caused by immigration would make our results conservative (i.e., Fig. 1), in addition to mimicking the open nature of natural streams. The mesh size at mesocosm outflows was fine enough (0.02 cm^2) to prevent emigration of salamanders and macroinvertebrates.

The PERMANOVA of CONTROL treatments indicated that the benthic and emerging macroinvertebrates sampled represented different communities, likely due to the phenology of emerging macroinvertebrates. The macroinvertebrates emerging in September likely represented a subset of the benthic community. There are two plausible explanations, then, for the finding that *G. porphyriticus* decreased benthic macroinvertebrate densities without affecting the density of emerging macroinvertebrates. First, the taxa *G. porphyriticus* fed on may not have emerged in September. Second, if *G. porphyriticus* fed on only a subset of taxa that emerged in September, this effect may not have been detectable within samples of all emerging macroinvertebrates (Reinhardt et al. 2017).

Our results add to mounting evidence that salamanders are influential components of headwater stream food webs. Specifically, this experiment shows that salamanders can exert top-down control on headwater food webs, which is consistent with model predictions (Atlas and Palen 2014). Our results also show that these top-down effects may be regulated by the assemblage of stream salamander species present, with intraguild predation resulting in risk reduction for shared benthic macroinvertebrate prey. As an important model system in community ecology, there is a wealth of knowledge on intraguild interactions among stream salamanders (Hairston 1980; Gustafson 1993; Jaeger et al. 1998; Bruce 2008). By demonstrating that these intraguild interactions are integral to understanding the role of salamanders in stream food webs, we hope this work opens new avenues of research on the direct and indirect effects of salamanders on community and ecosystem dynamics in headwater streams.

Acknowledgments.—We thank I. Halm (USDA Forest Service) for logistical support; A. Saenger, S. Luther, Z. Morrison, and M. McQuillan for field assistance; and L. Eby, N. Rodenhouse, J. Maron, R. Hauer, T. Wilcox, L. Swartz, C. Filardi, and B. Addis for comments on this manuscript. This research was funded by the National Science Foundation (DEB-1114804, DEB-1050459, DEB-1655653, and DEB-1637685) and was conducted under Montana State Institutional Care and Use Protocol number 003-14WLDBS- 012714. This is a contribution to the Hubbard Brook Ecosystem Study. The Hubbard Brook Experimental Forest is operated and maintained by the Northeastern Forest Research Station, USDA Forest Service, Newtown Square, PA.

Supplemental Material

Supplemental material associated with this article can be found online at https://doi.org/10.1655/Herpetologica-D-20-00022.T1 and https://doi.org/10.1655/Herpetologica-D-20-00022.T2

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Accepted on 13 January 2021
Associate Editor: Chris Gienger

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