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PREDATOR PRESENCE AND SIZE VARIATION ALTERS COMMUNITY STRUCTURE THROUGH MULTIPLE TROPHIC CASCADES

A Thesis
Presented to
the Faculty of the Department of Biological Sciences
Murray State University
Murray, Kentucky

In Partial Fulfillment
of the Requirements for the Degree
of Master of Science in Watershed Science

by Robin Stover Baker
June 2018

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ABSTRACT

Predation plays a crucial role in shaping community structure and can initiate trophic cascades that can alter abundances across adjacent trophic levels. Recent research has suggested that variation among individual predators may have stronger effects on ecological dynamics than previously appreciated. Intraspecific variation within predators could lead to differential levels of top-down control with implications for trophic cascade strength. In this experiment, we manipulated the body size variation of predatory mole salamanders (*Ambystoma talpoideum*) within experimental mesocosms and monitored a suite of abiotic and biotic response variables. We predicted that predator populations with increased body size variation would have limited top-down control due to weaker interactions with a greater number of prey species. Conversely, we predicted that populations with similarly sized predators would have strong control over fewer prey species. Salamander presence affected nearly every biotic parameter measured, suppressing some populations (e.g. invertebrate predators) and facilitating others (e.g. invertebrate collectors), triggering multiple trophic cascades. A few invertebrate taxa responded to variation in predator body size and in nearly all of these instances, taxa responded more strongly to treatments with increased body size variation than in treatments with similarly-sized predators. Predator size variation may promote individual dietary specialization by differently sized predators, resulting in strong control of focal prey. These results demonstrate that predators have pervasive effects on all trophic levels of a community regardless of size structure, and that when size structure has an effect on abundances of particular taxa, increased body size variation can lead to stronger top-down control.

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INTRODUCTION

Predation is a fundamental species interaction that shapes biological communities (Hairston et al. 1960, Sih et al. 1985). While the relative importance of top-down and bottom-up influences in regulating communities has been debated (Strong 1992, Polis 1999), trophic cascades are generally accepted as examples of strong top-down control (Pace et al. 1999). Trophic cascades are the processes by which predators exert a direct negative influence on a trophic level, which in turn releases lower trophic levels from predation or consumption, leading to cascading effects across trophic levels (Ripple et al. 2016).

Trophic cascades have been described in a variety of ecosystems, from forests (Terborgh et al. 2001, Ripple and Beschta 2003) to lakes (Carpenter et al. 2001, Ellis et al. 2011) to oceans (Frank et al. 2005, Casini et al. 2008). However, the strength and extent of these various trophic cascades can differ drastically both among and within ecosystems. Shurin & Borer (2002) examined reported trophic cascades in six terrestrial and aquatic ecosystems and found that differences in cascade strength within the surveyed aquatic systems were as great as the differences between terrestrial and aquatic systems. Factors suggested to contribute to observed variation in cascade strength includes the degree of 'reticularity' (diversity of species and number of linkages) within a whole food web (Strong 1992), diversity within trophic levels (Holt and Polis 1997), and inherent differences in species' biology (such as resource conversion efficiency) (Borer et al. 2005).

While many of these explorations of trophic cascades include diversity *among* species, few of these mechanisms explicitly compare variation of traits or behaviors *within* species. Yet, there is a growing recognition of the importance of intraspecific variation in community dynamics (Bolnick et al. 2011, González-Suárez et al. 2015, Keiser et al. 2015, Siefert and Ritchie 2016). Variation in traits or behaviors among individuals of a species can have profound implications on communities by altering the strength or number of species interactions, stabilizing populations against fluctuations of various phenotypes, and changing genetic and eco-evolutionary feedbacks (De Roos et al. 2003, Bolnick et al. 2011). Body size variation (i.e., size-structure) is a common source of intraspecific variation and can arise from ontogenetic shifts (Werner and Gilliam 1984), density and competitive regimes (Persson et al. 2003), or phenotypic variation. Body size is linked to many important ecological dynamics including metabolism, aggression, and consumption rates (Woodward et al. 2005).

Size-structure within predator populations in particular can have interesting and complex implications in an ecological community (Rudolf 2007, Rudolf and Rasmussen 2013a). Since there are many predatory traits linked to body size (such as foraging rates or gape size) that can have nonlinear relationships with ecological processes, the strength of predator control can vary among populations with different amounts of body size variation (Bolnick et al. 2011). In particular, the concept of Jensen's inequality points out that failing to account for individual variation in traits or interaction strength can lead to unrealistic ecological predictions (Ruel and Ayres 1999).

Size-structured populations may also be composed of individuals that have different or specialized niche requirements (Wilson 1975). As gape-limited predators

grow, the range of prey items available to them also increases and their niche broadens, leading to generalist populations composed of individual specialists that face reduced intraspecific competition (Woodward and Hildrew 2002, Bolnick et al. 2003, Svanbäck and Persson 2004, Lichstein et al. 2007). Additionally, cannibalism and intraguild predation are common among size-structured predator populations, with larger individuals preying on smaller individuals regardless of the species' overall trophic role (Holt and Polis 1997). Larger predators thus have a broader niche and wider range of available prey items that can include conspecifics. Under the mechanism of increased degree, predators that consume a greater variety of prey items (in this case, the largest predators) should exhibit weaker interactions with each prey, leading to weaker top-down control of any one prey species (Bolnick et al. 2011). The concepts of increased degree could be scaled up to state that predator populations that collectively consume a wide variety of prey also exhibit weaker top-down control. Conversely, a population with all similarly sized animals would concentrate on a similar range of prey items with a strong degree of top-down control on those prey species.

Several theoretical studies have explored the possible effects of size variation within predators on trophic cascades (Rudolf 2007, Miller and Rudolf 2011). However, relatively few empirical studies have been conducted to support these modeling efforts, and most have focused primarily on simple systems of invertebrate predators and prey (Rudolf and Rasmussen 2013b). Additionally, many examples of trophic cascades have involved large vertebrate predators such as wolves (Beschta and Ripple 2012) or otters (Estes and Duggins 1995). While these charismatic species do much to bring awareness to the phenomenon of trophic cascades, they are very difficult to manipulate on a

practical scale. Experiments involving smaller vertebrate predators may yield more tractable studies and generalizable results.

Mole salamanders (*Ambystoma talpoideum*) are an excellent model species to use in empirical investigations of body size variation effects on food web dynamics. Due to their facultatively paedomorphic life history, *A. talpoideum* are an inherently size-structured species (Doyle and Whiteman 2008). Paedomorphs are aquatic sexually mature adults that retain characteristics of larvae, such as gills. Both larvae and paedomorphs can also metamorphose into terrestrial adults that return to ponds to breed (Semlitsch 1985). Salamander populations living in ponds exhibit strong size structuring, ranging from newly hatched larvae (< 1 cm) to older adults reaching sizes of over 16 cm (R. Baker, personal observations). Paedomorphs act as top predators in fishless ponds, consuming a wide variety of prey, including zooplankton, macroinvertebrates, tadpoles, and conspecifics (Collins and Holomuzki 1984, McCallister and Trauth 1996, Whiteman et al. 1996, Wissinger et al. 1999). Since salamanders are gape-limited, the size and diversity of prey available to an individual salamander depends on its size.

Further, body size variation within salamanders could alter the nature of conspecific interactions with implications for top-down control. Cannibalism among size-structured salamanders is well documented (e.g. Nyman et al. 1993, Wissinger et al. 1999). Among ambystomatid salamanders, cannibals will consume conspecifics that are 50% or less of their own body size (Wissinger et al. 2010), although cannibalism has been observed at body size ratios as low as 20% (C. Mott, personal observation). Size structuring can also alter non-consumptive agonistic interactions. For instance, Brunkow and Collins (1996) observed evidence for increased aggression within populations of

similarly sized salamanders, and Mott and Maret (2011) noted that aggressive behaviors among salamanders could be driven by both external factors (such as body size) as well as inherent species-specific aggression. Reduced activity and/or foraging is a common response by organisms under threat of attack (e.g. Peckarsky et al. 1993, Davenport and Chalcraft 2013). All of these agonistic interactions, whether or not they result in cannibalism, could potentially alter predation pressure on lower trophic levels if salamanders respond to aggression/fear of cannibalism by reducing their foraging rates. Through this mechanism, body size variation in salamander populations could thus significantly influence invertebrate and primary producer community assemblages.

We used *A. talpoideum* to investigate the effect of body size variation within a top predator on trophic cascades in experimental pond communities. Because previous studies have shown that paedomorphic salamanders can be dominant predators, (Dodson 1974, Whiteman et al. 1996, Wissinger et al. 1999), we hypothesized that communities would be different between mesocosms with and without salamanders. Specifically, we predicted that salamander predation in our experimental ponds would be strong enough to trigger a trophic cascade by suppressing invertebrate populations and facilitating lower trophic levels.

Additionally, because theory suggests that niche breadth increases as both absolute individual body size and population size variation increases (Wilson 1975, Bolnick et al. 2011), we hypothesized that trophic cascades would weaken as variation in predator size increased. At low levels of size structure, we predicted that similarly sized salamanders would be limited to the same prey items, leading to a narrow niche breadth and increased predation on a smaller range of organisms, and resulting in strong top-

down control and a clear trophic cascade. Conversely, as predator size variation increased, the niche breadth of the predator population should also increase, leading to more diffuse top-down control and weaker cascades.

METHODS

Experimental Design

The experiment was conducted at Murray State University's Hancock Biological Station in western Kentucky. Each mesocosm was assigned one of three salamander treatments: high size variation ('High'), low size variation ('Low'), or no salamanders ('Control'). Mesocosms were divided into six blocks with two replicates of each treatment per block, for a total of 36 experimental mesocosms.

Experimental mesocosms were constructed in polyethylene plastic cattle tanks in early spring 2016, following previously established methods (Anderson and Whiteman 2015). Each tank was filled with 1000L of well water, 20 gallons (0.07 m^3) of leaf litter (primarily *Quercus* spp. and *Carya* spp. from nearby forests), two liters of phytoplankton-rich water from a nearby mesocosm array, and a total of one liter of concentrated zooplankton inoculations collected from nearby ponds and distributed among mesocosms over a period of three weeks. The entire experimental array was covered by a shade cloth from May to August that allowed 50% transmission of light and some precipitation to pass through, simulating natural shade conditions in a forest pond. Mesocosms were left uncovered to permit natural colonization of invertebrates. The establishment of the invertebrate, zooplankton, and algal communities were further supplemented by the addition of 10L of benthos (decomposed leaf litter and organic matter) that contained Odonata nymphs, larval Chironomidae, and gastropods, among other invertebrates. These benthic inoculations were collected from a nearby mesocosm array that had been constructed in similar fashion, but abandoned for one year.

Each tank received 10 leaf packs and 10 ceramic tiles to monitor decomposition and periphytic algae, respectively. Leaf packs were constructed by placing 5g of whole dried leaves into nylon mesh bags (Benfield 2006). The leaves were a multi-species homogenized mixture representative of benthic leaf litter in the mesocosms. All leaf packs were placed together in the same area of each tank directly on top of the benthic leaf litter. To provide an estimate of leaf mass lost due to handling error, six leaf packs were placed in tanks, immediately removed and frozen. Algal tiles were constructed by gluing 47 mm^2 unglazed rough porcelain onto nylon strings (Lamberti and Resh 1985). The ceramic tiles had been previously soaked in water and scrubbed clean to remove residual glue and chemicals. Tiles were suspended approximately one inch apart at the same height along northeastern side (facing southwest) of each tank.

Salamanders were collected from ponds in Calloway County, Kentucky and Carroll County, Tennessee. We collected from two populations to increase the number, as well as the diversity, of sizes of salamanders available for the experiment. We measured animals' snout-vent lengths (SVL), total lengths, and weights. We created three size classes based on the available numbers and SVLs of salamanders: small (26-31 mm SVL), medium (38-55 SVL), and large (58-63 SVL). Generally, salamanders from Carroll County, TN were bigger than the salamanders from Calloway County, KY and made up a higher proportion of the 'large' size class. High variation treatments received one salamander from each size class (1 small, 1 medium, 1 large), while low variation treatments each received three medium sized salamanders (Table 1). Salamanders were assigned to size groups without regard to their sex or original population. We maintained equal mean body sizes among size structure treatments, while significantly manipulating

the variation around each of these means (High treatment mean body size: 45.8 ± 0.7 mm, Low treatment mean body size: 46.4 ± 0.8 mm; $t = -1.96$, $df = 21.9$, $p = 0.06$. High treatment mean standard deviation: 16.1 ± 1.3, Low treatment mean standard deviation 5.3 ± 1.6; $t = 17.79$, $df = 21.0$, $p < 0.0001$).

The experiment commenced when salamanders were placed in tanks on April 14th, 2016. Tanks were monitored for metamorphs (identified by the reabsorption of gills), which were then removed due to their inefficient foraging skills and different dietary preferences than paedomorphs (Whiteman et al. 1996). When possible, metamorphs were replaced with similarly sized paedomorphs obtained from Carroll County, Tennessee. After five weeks we discontinued replacing metamorphs due to lack of available replacement animals and acknowledged realistic pond conditions in which animals naturally metamorphose and leave ponds (Doyle and Whiteman, 2008). Animals continued to metamorphose throughout the duration of the study. A final census was conducted upon completion of the experiment by trapping and thoroughly dipnetting for animals. Any salamanders caught were photographed and measured for SVL, total length, and weight. Salamanders were returned to their tanks following processing. All results were analyzed based on initial treatment, regardless of (sometimes unknown) changes in salamander densities throughout the experiment.

Monitoring the mesocosms

Mesocosms were monitored for a suite of abiotic and biotic parameters from April-September 2016. Five sampling events were conducted at approximately 1, 5, 8, 13, and 21 weeks post-salamander addition. Specifically, samples were taken April 22-

30, May 20-27, June 10-14, July 14-20, and September 11-14, 2016. During each of the sampling events, 14 environmental and biological parameters were measured. These parameters included temperature, pH, dissolved oxygen (DO), turbidity, oxidation-reduction potential (ORP), specific conductivity, soluble reactive phosphorous (SRP), nitrate/nitrites, periphyton, phytoplankton, zooplankton, benthic invertebrates from core samples, benthic invertebrates from leaf packs, and decomposition. Additional information on tadpoles and plant densities were obtained at times other than these principal five sampling events.

Physical water parameters- temperature, pH, DO, turbidity, ORP, and conductivity- were obtained using a multi-sensor sonde (Yellow Springs Incorporated, model 6820). We measured nutrient concentrations of nitrate/nitrites and SRP by first collecting water from the middle of the tank in the middle of the water column using a bottle sampler. 50 ml of this raw water sample was then filtered through a 0.45µm nylon filter, and samples were immediately frozen and analyzed within two weeks using a Quik Chem Flow Injection Analyzer at the Hancock Biological Station.

We measured two sources of chlorophyll-*a* in this study, phytoplankton and periphyton. To obtain phytoplankton samples, 250 mL of tank water was collected via a bottle sample and filtered through glass GF-F (0.7 µm) filters. Periphyton samples were obtained by scraping and rinsing all the algae off of a tile into a jar of distilled, deionized water that was then filtered through a glass GF-F filter. Each tile was sampled only once during the experiment. Filters for both periphyton and phytoplankton were frozen for a maximum of two weeks before processing. To determine chlorophyll concentrations, filters were ground with 10 mL of acetone to extract the chlorophyll pigment and

analyzed at Hancock Biological Station using a spectrophotometer (Beckman DU 640B) following methods established by the Environmental Protection Agency (Arar and Collins 1997).

Zooplankton were sampled using an 80 μm Nitex nylon mesh conical net (Fieldmaster® Mini-Net). The net was guided diagonally down from one edge of the tank to the opposite edge where it was hauled vertically up. This grab was performed once per tank in the initial April sample, and twice per tank in all subsequent samples, due to concerns about sampling efficacy. Liquid retained in the net's catch bottle was consolidated to approximately 30 mL and transferred to a tissue culture flask. 1.5 mL of carbonated soda water was added to each flask and allowed to sit for 10 minutes to relax organisms in the sample before fixing with enough 10% formalin to obtain a final concentration of 2-3%. Samples were dehydrated to achieve a standard volume of 30mL (Wetzel and Likens 1991, Eaton et al. 1998). The flask was gently disturbed to ensure homogenization of the entire sample before obtaining a 1mL subsample with a plastic pipette. Zooplankton within each 1 mL subsample were enumerated and identified to order using a Sedgwick-Rafter counting cell. This procedure was repeated 5 times for each sample, for a total of 5mL of subsample enumerated per sample.

Benthic invertebrates were sampled using a modified stovepipe core (Shaffer et al. 1994). Traditional benthic invertebrate collection using a stovepipe core requires a soft substrate in order to bury the base of the core, which the hard plastic base of the mesocosm did not provide. We modified a stovepipe core in such a way to ensure that it could stand upright on its own while we collected samples. To collect a benthic sample, we used our hands to grab three consistently sized handfuls of leaves and used a fine

mesh net to collect three scoops of the water column from within the core. Each handful was similarly sized, and if there was too little leaf litter to provide three full handfuls' worth, we collected all that remained within the core. Leaves and net contents were transferred to a 250 µm sieve, rinsed, then put into a Whirl-Pack and preserved with 10% formalin stained with Rose Bengal. We collected one benthic sample per tank per sampling event.

Benthic samples were later picked for macroinvertebrates by transferring the sample to a sieve series, rinsing, and discarding formalin waste. Contents of the largest sieve (4000 µm) were emptied into a white enamel tray and visually picked for macroinvertebrates. Large leaves were discarded, leaving small leaf fragments and microinvertebrates. This detritus was then re-filtered through two smaller sieves (2000 and 500 µm) and emptied into Petri dishes and inspected for invertebrates under a dissecting scope. All invertebrates were placed in 10% formalin, measured to the nearest mm using graph paper placed under the sample dish, and identified down to practical taxonomic resolution (generally to order, but occasionally to class) using Merritt and Cummins (2008). Biomass estimates were calculated by obtaining length-mass regressions for each taxa based primarily on Benke et al. (1999) as well as other references (Baumgärtner & Rothhaupt, 2003; Sabo et al., 2002; Stoffels et al., 2003; Supplemental Table 1).

Decomposition was monitored by measuring the rate of mass lost from the pre-weighed leaf packs after adjusting for the handling error based on the six leaf packs reserved for this calculation (Benfield 2006). During each sampling event, we removed a single leaf pack from each tank and immediately froze it. To obtain ash-free dry mass, the

leaves were thawed in water, carefully rinsed, placed into a metal pan, and dried at 50°C for 48 hours. Following drying, the leaves were weighed, ground to a powder, and a 1 mg subsample was ashed in a muffle furnace at 550°C for one hour to remove all organic material. The percent organic matter was calculated from the difference in weights between the dry, pre-ashing and ash-free mass subsamples. This percent organic matter was multiplied by the dry weight of the full sample to obtain an overall ash-free dry mass for each leaf pack.

Leaf packs were also sampled for macroinvertebrates. After removing all leaf material from a sample, we picked the remaining detritus for invertebrates, then rinsed the detritus through a 250 µl sieve, transferred to a plastic Petri dish and picked under a dissecting scope. All invertebrates were placed in 10% formalin, measured to the nearest mm, and identified to order or family. Biomass estimates were obtained using published length-mass regressions as previously described.

All invertebrates from the benthos and the leaf packs were assigned to one of four functional feeding groups; predator, collector, grazer, or filterer (Merritt & Cummins, 2008). The predator functional feeding group primarily consisted of Hydrophilidae beetle larvae, Anisoptera nymphs, and Ceratopogonidae larvae, with few instances of larval Dytiscidae beetles, Chaoboridae, and others. Collectors primarily consisted of Chironomidae larvae, Oligochaeta, Ephemeroptera larvae and Trichoptera larvae. We only found three families of grazers in the mesocosms: Physidae, Lymnaeidae and Ancylidae, and only one filterer: Ostracoda. The feeding group assignments for all taxa found in the mesocosms are presented in Supplemental Table 1.

Oligochaeta were only counted for abundance purposes if a head could be identified, and only measured for biomass purposes if they were intact; segments were not counted. Small gastropods (< 3 mm) that included limpets and young snails were lumped, since it was often difficult to conclusively differentiate them. However, individuals in this category were most frequently freshwater limpets (Ancylidae) with only a small proportion being snails. Ostracoda in each sample were counted but not measured since all were less than 1 mm and there was very little size variation. Both exuvia and bodies of Chironomidae, Ephemeroptera, Dytiscidae, and Hydrophilidae were included in their respective enumerations, because it was often difficult to conclusively differentiate between exuviae and larvae. Exuvia of other taxa were not included in abundance counts.

When mesocosms were initially stocked with supplemental benthos, *Utricularia* spp. (bladderwort) was unintentionally introduced into the tanks. *Utricularia* is a carnivorous aquatic plant that can feed on anything small enough to be captured by its mechanically-triggered bladders, primarily zooplankton and small dipteran larvae (Guiral and Rougier 2007). Indeed, bladderwort can be an effective enough predator to compete with other vertebrate predators, such as bluegill (Davenport and Riley 2017). Bladderwort also forms floating mats of vegetation that can support large amounts of periphytic algae, which subsequently provides shade to the mesocosm (Harms 2002). Between predation on invertebrates and shading of primary producers, there was potential for the bladderwort to significantly affect the mesocosm communities. Thus, we quantified the surface area of the mats by drawing maps of the vegetation for each tank, differentiating between areas of bladderwort and algae. We used a nylon twine grid

overlaid on each tank as a guide for drawing accurate sizes and shapes of bladderwort and algae on a paper template. Polygons representing bladderwort and algae were quantified in ImageJ (Schneider, Rasband, & Eliceiri, 2012; http://rsb.info.nih.gov/ij) to obtain vegetation surface area measurements among tanks. We conducted this vegetation inventory four times through the duration of the experiment, roughly monthly (May 31, June 28, July 25, August 30).

Tadpoles were another unplanned addition to the mesocosms' ecosystems. Frogs began naturally colonizing the tanks in late April, beginning with Cope's grey tree frogs (*Hyla chrysoscelis*), gradually transitioning to green tree frogs *(Hyla cinerea)* and finally southern leopard frogs (*Lithobates sphenocephalus*) by September. At the beginning of the experiment, any embryos detected in experimental tanks were removed and placed in a non-experimental reservoir tank. Eventually, it became inefficient to keep up with the number of egg masses deposited every night and to be certain that all masses were removed. We discontinued removing embryos after two weeks and allowed frogs to colonize tanks naturally. We monitored tadpole populations beginning in May. We took advantage of the even and consistent placement of the strings attached to the periphyton tiles, which created a 30x40 cm quadrat within which any tadpoles present were counted. Tadpole surveys were taken nearly every week from May 26 to September 7, 2016.

Statistical Analyses

All analyses were conducted in R version 3.3.1, and we used packages lme4, MASS, car, lsmeans, and ggplot2 throughout (R Core Team 2016, Venables and Ripley 2002, Wickham 2009, Bates et al. 2015, Lenth 2016). To answer questions about the

effects of salamander body size variation on the mesocosm community, we applied a series of generalized linear mixed models (GLMMs) on each of the 16 parameters sampled within the mesocosms (Bolker et al. 2009). To test the direct effects of salamander body size variation treatments on each response variable, we constructed a GLMM model using Date, Salamander Treatment, and their interaction as predictors, with block as a random effect. A handful of additional GLMM models used another measured variable as a predictor, e.g. we modeled periphyton concentrations with tadpole abundances (a measured variable) along with salamander treatment, date, and salamander*date interaction. Again, salamander treatments were coded as 'High' (high size variation), 'Low' (low size variation), and 'Control' (no salamanders). Main text tables 2 and 3 and Supplemental Tables 2, 3, and 4 provide a full list of response variables tested and outcomes of the GLMM.

We conducted an analysis of deviance using Wald Chi-Square tests to evaluate the significance of each main effect and interaction. We confirmed the importance (or lack thereof) of the interaction term comparing a full model with interaction term and a reduced model without the interaction term and evaluating if the interaction term significantly contributed to explaining more variation in the data. In all but one instance, the significance of the interaction term from the analysis of deviance agreed with results from model comparison. In the one model (Periphyton) where results differed, we opted to include the interaction term based on model comparison results and visual examination of the interaction plot. We also calculated a standard diversity index, the Simpson index, for the abundance data from the leaf pack and benthos samples. We compared similarities

between the invertebrate communities found in the leaf packs and benthos by calculating a Jaccard similarity index.

Examination of the data revealed that few of the response variables were normally distributed and/or homoscedastic. However, specifying alternate distribution families in GLMM's can alleviate concerns associated with non-normality (Bolker et al. 2009). In general, count data (zooplankton, invertebrate abundance), were modeled most commonly as a Poisson distribution and in a few instances, as a lognormal distribution. Continuous data were modeled with either normal, lognormal, or gamma distributions. For instances where several distribution families could be used to model a response variable, only the best-fitting family is reported here. Several models failed to converge, but these issues were resolved by adding a constant (usually 1 or 0.1) to the response variable, by using a bobyqa (Bound Optimization By Quadratic Approximation) optimizer instead of the default Nelder-Mead optimizer, by specifying starting values, and/or by scaling the response variable. The specific family distributions and model adjustments for each response variable can be found in Supplemental Table 5. There were very few instances of missing data and since GLMM's are robust to missing and unbalanced data, none of the analyses were likely severely affected by missing observations (Bolker et al. 2009).

In order to compare response variables across time we aligned the dates of the tadpole and bladderwort samples to match the dates of the other main samples. For tadpoles, we averaged the counts from the three weeks prior to each main sampling event to give an estimate of tadpole abundances during each main sample. That is, tadpole counts from May 26, June 1, and June 7 were averaged to give an estimate of tadpole

abundances during the June sample. Tadpole counts from June 22, July 1, and July 13 were averaged to create a July sample, and August 24, August 31, and September 7 were averaged for a September sample. Bladderwort surveys were conducted four times, in May 31, June 28, July 25, and August 30. Data from each bladderwort sample were assigned to the closest main sampling event, with the assumption that surface area of the bladderwort did not significantly change during the time interval between the bladderwort sample and the main sample.

RESULTS

Salamanders

In the first month of the experiment, we attempted to maintain initial densities and size variation by replacing any metamorphosing salamanders with similarly sized individuals. During this replacement period, we lost 32 salamanders from the tanks. Of these 32 salamanders, 23 (72%) came from mesocosms in the Low treatment and were thus all 'medium' sized salamanders (see Methods for a description of how we classified the sizes of salamanders). The remaining nine salamanders (28%) came from High treatment mesocosms. Six of these were 'large' salamanders, one was a 'medium' and we were unable to conclusively determine the toe clips and thus the size class of two salamanders. By the conclusion of the replacement period, 68 out of 72 total salamanders remained in the mesocosms, a retention rate of 94% (with replacement) and 6% loss rate. We were unable to replace four salamanders due to lack of replacement individuals. These four individuals were all 'large' salamanders from the High size variation tanks. By the end of the experiment, only 36 out of these 68 salamanders remained, a 47% loss of salamanders due to metamorphosis, death, or detection error. These 36 remaining salamanders were nearly evenly split between the two body size treatments: 17 (47%) remained in the High size treatment, while 19 (52%) remained in the Low treatment. However, loss of salamanders was distributed differently within the two body size treatments (Supplemental Figure 1). In the Low treatment, there was an even distribution of remaining salamander populations- that is, there were three mesocosms each with one, two, three, or no salamanders left. However, in mesocosms with High size variation

treatment, final populations primarily consisted of either one or two salamanders. Only one tank in the High size variation treatment had all three salamanders remaining and only one tank lost all three salamanders. We are unable to provide data on which individual salamanders remained or probabilities of losing a 'large' or 'small' salamander. However, at the end of the experiment, mean body sizes in the tanks remained similar between treatments (t = 0.85, df = 14.6, p = 0.4), but there was no longer a difference in variation around each of these means between treatments (t = 0.3, df = 15.0, p = 0.76).

Tadpoles

Tadpole abundances were significantly affected by salamander treatment ($\chi^2 = 153.5, \mathrm{df} = 2,$ p < 0.0001), date ($\chi^2 = 177.4$, df = 11, p < 0.0001), and the salamander*date interaction ($\chi^2 = 53.6$, df = 22, p = 0.009). Tadpole abundances were significantly higher in the Control treatment than either the High (p < 0.0001) or Low (p < 0.0001) treatments. Abundances in all treatments were highest in the early sample dates and declined over time (Table 3, Figure 1B).

Leaf Packs: Invertebrate Community Abundances

We counted 46,433 invertebrates from the leaf packs and of these, we individually measured 10,496 individuals. Leaf pack invertebrate communities consisted of 19 identified taxa and were dominated by Ostracoda, Ancylidae, and Chironomidae (Supplemental Figure 2). Total abundances of invertebrates in leaf packs were significantly affected by salamander treatment (χ^2 = 305.7, df = 2, p < 0.0001), date (χ^2

= 600.2, df = 3, $p < 0.0001$), and their interaction (χ^2 = 1168.4, df = 6, $p < 0.0001$; Table 2). Specifically, there were significantly fewer invertebrates in the High treatment than either the Low or the Control treatments ($p < 0.0001$ for both High-Low and High-Control contrasts). There was no significant difference in total invertebrate abundances between the Control and Low treatments ($p = 0.09$). All months were significantly different from one another at $p < 0.0001$ except June and September ($p = 0.48$). The most obvious interaction between size classes over time occurred between June and July, where the abundances in the Control treatment dramatically increased in July and became more abundant than the other two treatments in September.

Further investigation revealed that the overall trends of the total abundances were driven by shifts in Ostracoda. Ostracoda made up 86% of the total invertebrate abundances (but only 34% of the total biomass). Interaction plots of Ostracoda abundances and total benthic invertebrate abundances were virtually identical. Ostracoda were also significantly affected by salamander treatment (χ^2 = 720.1, df = 2, $p < 0.0001$), date (χ^2 = 1257.8, df = 3, $p < 0.0001$), and their interaction (χ^2 = 1140.1, df = 6, $p < 0.0001$). Ostracoda abundances among three salamander treatments and all four months were all significantly different from one another ($p < 0.0001$), an even stronger difference among treatments than in the total invertebrate analysis. Specifically, overall Ostracoda abundances were highest in the Control, then the High, then the Low treatment (all $p < 0.0001$). Abundances were highest in July, then September, June, and May (all $p < 0.0001$). However, overall Ostracod abundance trends across treatment and date are complicated by a sharp increase of abundances in the Control treatment from June to July.

Ostracods are small (<1mm) crustaceans and have been found in the gut contents of many fish and amphibian larvae (Mittelbach 1981, Collins and Holomuzki 1984, Schiesari et al. 2009), including *A. talpoideum* (Taylor et al. 1988). However, little is known of the electivity, or preference, for Ostracoda by larger *A. talpoideum* larvae or paedomorphs. That is, it is unclear whether Ostracoda are intentionally consumed or accidentally ingested with other prey items. Further, Ostracoda have been observed surviving ingestion and digestion by fish, suggesting that these small crustaceans may not make a large energetic contribution to diet of fish or amphibians (Vinyard 1979). In order to investigate trends among remaining taxa, we eliminated Ostracods and reexamined total remaining invertebrate abundances.

Total invertebrate abundances in the leaf packs after excluding Ostracoda still revealed significant effects of salamander treatment (χ^2 = 251.6, df = 2, p < 0.0001), date (χ^2 = 367.1, df = 3, p < 0.0001), and the salamander*date interaction (χ^2 = 62.1, df = 6, p < 0.0001; Table 2, Supplemental Figure 3). Invertebrate abundances without Ostracoda were significantly lower in Control treatments than in either the High (p = 0.0007) or Low (p = 0.0006) salamander treatments, and there was no difference between High and Low treatments (p = 0.99). Abundances generally decreased over time in all three treatments, and there were three significant pairwise contrasts of months (May-July, p = 0.0007; May-September, p < 0.0001; June-September, p = 0.0003).

Invertebrate predators were significantly affected by salamander treatment (χ^2 = 15.6, df = 2, p < 0.0001), date (χ^2 = 60.5, df = 3, p <0.0001), and their interaction (χ^2 = 19.2, df = 6, p = 0.004; Figure 2A). Predators in the Control treatments were significantly more abundant than in the salamander-present treatments (Control-High, p < 0.0001 and

Control-Low, $p = 0.02$) but there was no difference between the High and Low treatments ($p = 0.15$). There was also a significant effect of date on the predators, with predators being significantly more abundant in May than all other months ($p < 0.0001$). No other months were significantly different from one another. Finally, the significant interaction between date and salamander treatment was due to a convergence of predator abundances in September, such that abundances of invertebrate predators in the Low and High treatments increased from July and abundances of the predators in the Control treatment decreased over the same period.

Collector abundances in the leaf packs were also significantly affected by salamander treatment ($\chi^2 = 236.2$, df = 2, $p < 0.0001$), date ($\chi^2 = 206.5$ df = 3, $p < 0.0001$), and the salamander*date interaction ($\chi^2 = 40.2$, df = 6, $p < 0.0001$; Figure 2C). Collectors were significantly less abundant in the Control treatments than in either of the salamander treatments ($p < 0.0001$ for both Control-High and Control-Low). There was no difference in abundances between High and Low treatments ($p = 0.99$). All pairwise month contrasts were significant except for one, between June and July ($p = 0.63$). The significant salamander*date interaction was likely driven by the different months at which each treatment reached their lowest abundances. That is, in all treatments, collector abundances dropped from May to June, but continued to decrease from June to July in the control treatment, while the High and Low treatments remained steady or increased, respectively. Abundances in all three treatments increased from July to September, but abundances in the Control treatment remained lower across all four months. Trends in the collector functional feeding group in the leaf packs were driven primarily by

Chironomidae larvae. Predators, specifically Hydrophilidae larvae, had a significant negative effect on collector abundances (χ^2 = 4.6, df = 1, p = 0.03, Figure 3).

Grazers were also significantly affected by salamander treatment (χ^2 = 60.6, df = 2, p < 0.0001), date (χ^2 = 782.4, df = 3, p < 0.00001), and the salamander*date interaction (χ^2 = 93.3, df = 6, p < 0.0001; Figure 2E). Abundances of grazers in the Control treatment were significantly lower than in either of the salamander-present treatments (p < 0.0001 for both Control-High and Control-Low). There was no significant difference between the High and Low treatments (p = 0.99). All months were significantly different from one another (all p < 0.0001) for each pairwise contrast.

Examination of the Simpson diversity index revealed a significant effect of salamander treatment (χ^2 = 7.2, df = 2, p = 0.02) and date (χ^2 = 38.1, df = 3, p < 0.0001), but no interaction effect (χ^2 = 11.4, df = 6, p = 0.07) on invertebrate diversity in the leaf packs. Diversity levels were similar among the three treatments in May and June. From June through July, diversity declined in the Control treatment, while it remained relatively stable in the salamander-present treatments. However, the only significant pairwise differences in diversity are between the less diverse Control treatment and the High treatment (p = 0.02). There was no significant difference between Control-Low (p = 0.32) or High-Low treatments (p = 0.43).

Leaf Packs: Invertebrate Community Biomass

Total invertebrate biomasses from the leaf packs were significantly affected by salamander treatment (χ^2 = 6.2, df = 2, p = 0.04) and by date (χ^2 = 21.8, df = 3, p < 0.0001), but not by their interaction (χ^2 = 6.2, df = 6, p = 0.4; Figure 4B, Table 2). No

significant pairwise contrasts of salamander size class treatment were revealed. Only three pairwise contrasts showed significant differences in total biomasses among months, and all three of these included July, which had significantly higher biomasses than the other months. Specifically, May-July (p = 0.03), June-July (p = 0.008, and July-September (p = 0.003) all had significantly different invertebrate biomasses.

After excluding Ostracoda, total invertebrate biomasses were not significantly affected by salamander treatment (χ^2 = 4.0, df = 2, p = 0.13) or the salamander*date interaction (χ^2 = 3.2, df = 6, p = 0.79). However, the biomasses were significantly affected by date (χ^2 = 20.75, df = 3, p = 0.0001), with significantly higher biomasses in July than in June (p = 0.03) or September (p = 0.01).

Invertebrate predator biomass was significantly affected by sample date (χ^2 = 20.7, df = 3, p = 0.0001), but not by salamander treatment (χ^2 = 3.7, df = 2, p = 0.15) or a salamander*date interaction (χ^2 = 4.8, df = 6, p = 0.56; Figure 2B). Only two pairwise contrasts of date were not significant. May and September (p = 0.98) and June and July (p = 0.96) did not have significantly different predator biomasses, while all other contrasts did. May and September had similarly high biomass levels, while June and July had lower levels of biomass. While there was no significant effect of salamander size class treatment, mean biomasses in the Control treatment were higher than mean biomasses of the salamander-present treatments in all months.

Collector biomass was significantly affected by salamander treatment (χ^2 = 25.1, df = 2, p < 0.0001) and date (χ^2 = 30.4, df = 3, p < 0.0001), but not their interaction (χ^2 = 3.7, df = 6, p = 0.72; Figure 2D). Collector biomass was significantly lower in the Control treatments than either the High (p = 0.001) or the Low (p = 0.0002) salamander-

present treatments. There was no difference in biomass between the High and Low treatments (p = 0.80). Biomasses in May were not significantly different than biomasses in either June (p = 0.77) or July (p = 0.31). Biomasses were significantly different among all other months, with September having markedly lowest collector biomass.

Grazer biomass was significantly affected by salamander treatment (χ^2 = 8.6, df = 2, p = 0.01) and date (χ^2 = 21.5, p < 0.0001), but not the interaction (χ^2 = 3.9, df = 6, p = 0.68; Figure 2F). There were no significant pairwise contrasts among salamander treatments. Only two pairwise contrasts of months had significantly different grazer biomasses: July had significantly higher grazer biomass than either May (p = 0.03) or June (p = 0.04).

Ostracod biomasses were significantly affected by salamander size class treatment (χ^2 = 8.8, df = 2, p = 0.01) and sample date (χ^2 = 12.2, df = 3, p = 0.007), but not their interaction (χ^2 = 10.2, df = 6, p = 0.1; Figure 2H). No significant pairwise contrasts of size class were revealed, and there was only one significant contrast of date (May-July, p = 0.008).

Benthos: Invertebrate Community Abundances

The benthic invertebrate community was similar but not identical to the community sampled in the leaf packs, with an overall Jaccard similarity index of 89%. The benthic invertebrate community consisted of 18 identified taxa, and over 32,947 individuals were counted and measured. Oligochaeta and Chironomidae dominated the benthic community. While the leaf pack and benthic communities had high abundances

of Chironomidae in common, the benthos samples had much higher abundances of Oligochaeta and nearly no Ostracoda.

Total abundances of benthic invertebrates were significantly affected by salamander treatment (χ^2 = 870.9, df = 2, p < 0.0001), date (χ^2 = 5499.9, df = 4, p < 0.0001), and the salamander*date interaction (χ^2 = 218.4, df = 8, p < 0.0001; Table 2, Figure 4C). There were significantly fewer invertebrates in the Control treatment than either the High or Low salamander size class treatments (p < 0.0001 for both Control-High and Control-Low). There was no significant difference in abundances between the High and Low treatments (p = 0.61). All but one pairwise contrast of months was significant at p < 0.0001. There was no difference in invertebrate abundances from the benthos between June and July. Abundances were extremely low for all three treatments in April and rose sharply in May. Abundances in the High and Low treatments were significantly higher than abundances in the Control treatment in July and September (p < 0.001 for all).

The benthic invertebrate predator abundances were only affected by sample date (χ^2 = 412.9, df = 4, p < 0.0001), not salamander treatment (χ^2 = 1.2, df = 2, p = 0.54) or the salamander*date interaction (χ^2 = 3.9, df = 8, p = 0.87; Figure 5A). All but two pairwise contrasts of date were significant (p < 0.0001). Abundances of predators between May-June (p = 1.0) and July-September (p = 0.22) were not significantly different. Overall, abundances in all three treatments were very low in April, slightly higher in May and June, then rose sharply from June to July and remained high in September.

Collectors were significantly affected by salamander treatment (χ^2 = 814.4, df = 2, p < 0.0001), date (χ^2 = 6200.9, df = 4, p < 0.0001), and their interaction (χ^2 = 202.9, df = 8, p < 0.0001; Figure 5C). Abundances of collectors were significantly lower in the Control treatment than either of the two salamander-present treatments (p < 0.0001 for both Control-High and Control-Low). There was no significant difference in collector abundances between the High and Low treatments (p = 0.08). All pairwise contrasts of date were significant (p < 0.0001). Additionally, when predator abundances, specifically Hydrophilidae larvae abundances, were included in a GLMM model, they had a significant effect on collectors (χ^2 = 437.7, df = 1, p < 0.0001). Similarities between the model results and graphs for both the overall total abundances and the collector group indicate that total benthic invertebrate abundances were driven by collectors, which in turn were driven by the Oligochaeta and Chironomidae communities.

Grazers were significantly affected by salamander treatment (χ^2 = 114.1, df = 2, p < 0.0001), date (χ^2 = 649.1, df = 4, p < 0.0001), and their interaction (χ^2 = 201.4, df = 8, p < 0.0001; Figure 5E). Grazer abundances were significantly higher in the Control treatment than in High salamander size class treatments (p = 0.002). There was no significant difference in grazer abundances between Control and Low (p = 0.42) and High and Low (p = 0.25) treatments. All but one pairwise contrast of date was significant (p < 0.0001). Only June and July did not have significantly different abundances of grazers (p = 0.38).

Diversity of invertebrates in the benthos, as calculated by the Simpson index, was only significantly affected by date (χ^2 = 20.0, df = 4, p = 0.0004; Supplemental Table 4). Diversity in May was significantly lower than in June, July, or September. Neither the

salamander treatment (χ^2 = 1.4, df = 2, p = 0.47) nor the salamander*date interaction (χ^2 = 6.6, df = 8, p = 0.57) had a significant effect on diversity of benthic invertebrates.

Benthos: Invertebrate Community Biomass

Total biomass for the benthic invertebrates was significantly affected by date (χ^2 = 42.4, df = 4, p < 0.0001), but not salamander treatment (χ^2 = 0.7, df = 2, p = 0.7) or a salamander*date interaction (χ^2 = 9.6, df = 8, p = 0.29; Table 2, Figure 4D). Biomasses in all three treatments were significantly lowest in April, and there were no significant pairwise differences among the remaining months.

Benthic predator biomass was significantly affected by sample date (χ^2 = 30.6, df = 4, p < 0.0001), but not salamander treatment (χ^2 = 4.2, df = 2, p = 0.12) or the salamander treatment* date interaction (χ^2 = 10.4, df = 8, p = 0.27; Figure 5B). Four pairwise contrasts of date showed significant differences in biomass (p < 0.0001). These four contrasts all included April, that had significantly lower predator biomasses than all other months, and there were no significant differences in biomass among the remaining four months.

Salamander treatment (χ^2 = 9.0, df = 2, p = 0.01) and date (χ^2 = 68.3, df = 4, p < 0.0001) both had a significant effect on collector biomass in the benthos (Figure 5D). There was no significant salamander*date interaction on collector biomass (χ^2 = 4.0, df = 8, p = 0.85). There were no significant differences of collector biomass among salamander treatments. May had significantly higher collector biomasses than April (p = 0.002), July (p = 0.0008), and September (p = 0.0002). There were no significant differences among the remaining months.

Overall grazer biomasses in the benthos were not significantly affected by salamander treatment (χ^2 = 2.3, df = 2, p = 0.3), date (χ^2 = 5.8, df = 4, p = 0.21), or their interaction (χ^2 = 5.7, df = 8, p = 0.68; Figure 5F).

Zooplankton

Zooplankton abundances were significantly affected by salamander treatment (χ^2 = 50.7, df = 2, p <0.0001), date (χ^2 = 499.5, df = 4, p < 0.0001), and their interaction (χ^2 = 109.7, df = 8, p < 0.0001; Table 3, Supplemental Figure 4). The relative abundances among treatments varied by the month, and no one treatment had consistently higher or lower overall abundances across all sample dates. Yet, all three pairwise contrasts between salamander treatments were significant (Control-High: p = 0.0001, Control-Low: p = 0.004, High-Low: p = 0.0001) as were nearly all pairwise contrasts between months were significant (p < 0.0002). Only April and July did not have significantly different zooplankton abundances. Zooplankton abundances increased from April to May and decreased from May to September, with a sharp peak in the Control treatment in July.

When broken down by major zooplankton groups (Cladocera, Copepod, Copepod nauplii, and Rotifera), these general trends remained significant. That is, salamander treatment, date, and their interaction were all significant for Cladocera, Copepods, and nauplii when analyzed separately (Cladocera, salamander treatment: χ^2 = 22.1, df = 2, p < 0.0001; date: χ^2 = 376.9, df = 4, p < 0.0001; salamander*date: χ^2 = 43.2, df = 8, p < 0.0001. Copeopoda, salamander treatment: χ^2 = 42.1, df = 2, p < 0.0001; date: χ^2 = 369.7, df = 4, p < 0.0001; salamander*date: χ^2 = 141. 9, df = 8, p < 0.0001. Nauplii:

salamander treatment: χ^2 = 54.8, df = 2, p < 0.0001; date: χ^2 = 781.1, df = 4, p < 0.0001; salamander*date: χ^2 = 78.8, df = 8, p < 0.0001).

Cladoceran abundances were significantly higher in the High treatment than in the Control treatment (p = 0.02), but there were no differences between Control-Low (p = 0.44) and Low-High (p = 0.44). All month pairwise contrasts of Cladoceran abundances were significant (all p < 0.01). Cladoceran abundances in both the High and Low salamander treatments increased from April to June and declined from June to September. Cladocera in Control treatments also increased from April to May but declined after May.

Copepod abundances were significantly different between the Low-Control and Low-High treatments (p < 0.0001 for both), but not between the Control-High treatment (p = 0.98). All but two month contrasts were significant at p < 0.0001. There were no significant differences in copepod abundances between April-May and June-September. Copepods in all treatments generally increased together from April to July and declined from July to September with two exceptions. In July, the copepod abundances in the Control treatment dramatically increased above the other two treatments, and increased from July to September in the High treatment, where the other two treatments declined in the same time period.

Nauplii abundances peaked in May and declined through September. All pairwise contrasts between months were significant. Across all months, there were significantly fewer nauplii in the High treatment (Control-High and Low-High both p < 0.0001). There was no difference between the Control and the Low treatments (p = 0.11).

Rotifer abundances were relatively much lower than the other zooplankton. Rotifer abundances were significantly predicted by salamander treatment (χ^2 = 0.04, df = 2, p = 0.04), date (χ^2 = 237.8, df = 4, p < 0.0001) and their interaction (χ^2 = 22.8, df = 8, p = 0.003). Rotifers appeared most frequently in the earlier months, especially April, then sharply declined and were barely detectable by September. Despite the significance of the overall salamander treatment effect, there were no significant pairwise contrasts (all p > 0.5).

Primary Producers

Phytoplankton biomass was significantly affected by sample date (χ^2 = 14.2, df = 4, p = 0.006) but not the salamander*date interaction (χ^2 = 6.9, df = 8, p = 0.53; Table 3, Supplemental Figure 5). Overall salamander treatment had a significant effect on phytoplankton biomasses (χ^2 = 15.5, df = 2, p = 0.0004), but biomasses dramatically varied over time in the High treatment, and fluctuated to a lesser degree in both Control and Low treatments. Overall, phytoplankton biomass in the High treatment was significantly higher than in the Control treatment (p = 0.02) and there was no difference between the Low treatment and either High (p = 0.79) or Control (p = 0.07) treatments. However, in May and July, the phytoplankton concentrations were much higher in the High treatments than the other two treatments. In the other three months (April, June, September) the phytoplankton biomass among all three treatments was similarly low.

Periphyton concentration was not significantly affected by salamander treatment (p = 0.95), date (p = 0.72) or the salamander*date interaction (p = 0.64). However, examination of the interaction plot revealed that in May and June periphyton biomasses

were markedly lower in the Control treatments than in either High or Low treatments, and there was high variability within the High and Low treatments (Figure 1D). A GLMM model conducted on periphyton samples from only May and June revealed a significant effect of salamander treatment (χ^2 = 9.98, df = 2, p = 0.007) but no significant effect of date (χ^2 = 0.0001, df = 1, p = 0.99) or the salamander*date interaction (χ^2 = 1.0, df = 2, p = 0.61). That is, periphyton biomass was significantly lower in Control treatments than in either High (p = 0.004) or Low (p = 0.003) treatments in both May and June. Periphyton biomasses among all treatments were not significantly different in July and September (p < 0.05 for all). When included in a GLMM model, tadpole abundances had a significant effect on periphyton (χ^2 = 9.2, df = 1, p = 0.002), but Physid snail abundances did not (χ^2 = 0.004, df = 1, p = 0.94).

Bladderwort

Total surface coverage of bladderwort and algal mats together were significantly different among salamander treatments (χ^2 = 6.9, df = 2, p = 0.03; Supplemental Table 2, Supplemental Figure 6). Surface coverage in the High treatment was significantly higher than coverage in the Control treatment (Control-High, p = 0.001; High-Low, p = 0.17; Control-Low, p = 0.11). There was a significant overall effect of date (χ^2 = 79.1, df = 3, p < 0.0001), with May having a significantly lower amount of surface coverage than any of the other three months (p < 0.0001 for all). None of the other months were significantly different from each other. There was no interaction effect of salamander treatment and date (χ^2 = 8.8, df = 6, p = 0.18).

Bladderwort was the largest component of surface area coverage in the mesocosms, with algal mats constituting a smaller proportion. However, neither of these alone were significantly affected by salamander treatment (bladderwort, χ^2 = 4.3, df = 2, p = 0.11; algae, χ^2 = 2.6, df = 2, p = 0.27) or the interaction between salamander treatment and date (bladderwort, χ^2 = 11.4, df = 6, p = 0.07; algae, χ^2 = 5.4, df = 5, p = 0.49). Both bladderwort and algae alone were significantly affected by sample date (bladderwort, χ^2 = 90.1, df = 2, p < 0.0001; algae, χ^2 = 16.1, df = 3, p = 0.001). Bladderwort surface area coverage generally increased over time, while algal coverage peaked in June and declined afterward.

Leaf Packs: Decomposition

Decomposition rates, measured through loss of ash free dry mass of leaves contained within in leaf packs, were very similar among all treatments, and there was no significant effect of treatment on percent leaf mass loss (χ^2 = 4.6, df = 2, p = 0.1; Supplemental Table 2, Supplemental Figure 7). Ash-free dry mass declined significantly over time (χ^2 = 589.5, df = 3, p < 0.0001) and all pairwise contrasts of months were significant (p < 0.0001). Percent leaf mass remaining declined from 100% in April, to 88% in May, 82% in June, 75% in July and 65% in September. There was no salamander*date interaction (χ^2 = 4.8, df = 6, p = 0.57).

Water Quality

Out of eight measured water quality parameters only two, conductivity and soluble reactive phosphorous, were affected by salamander treatment (conductivity, χ^2 =

13.1, df = 2, p = 0.001; SRP, χ^2 = 9.6, df = 2, p = 0.008; Supplemental Table 2, Supplemental Figure 8). Conductivity was significantly higher in High size variation tanks than Low treatments across all five months (p = 0.002). There was no difference in conductivity between tanks without salamanders and either of the salamander-present treatments (both p = 0.19). Conductivity was significantly influenced by sample date (χ^2 = 518.9, df = 4, p < 0.0001). Specifically, conductivity values were significantly different (p < 0.05) among all but two months: only May and July (p = 0.18) and May and September (p = 0.98) were not significantly different from each other. There was no significant interaction effect between salamander treatment and date on conductivity (χ^2 = 1.4, df = 8, p = 0.9).

SRP was significantly affected by both salamander treatment (χ^2 = 9.6, df = 2, p = 0.008) and date (χ^2 = 146.7, df = 4, p < 0.0001), but not their interaction (χ^2 = 3.5, df = 8, p = 0.9). Initial levels of SRP in the mesocosms, measured in April, were highest in High size variation treatment, lowest in the Low size variation treatment, and intermediate in the Control treatment. Levels of SRP were also significantly highest in April and declined sharply to May, where there was no significant difference among the last four months.

None of the rest of the seven water quality parameters (nitrates/nitrites, dissolved oxygen, turbidity, pH, oxidation-reduction potential, and temperature) were significantly affected by salamander treatment. (Nitrates/nitrites, χ^2 = 2.1, df = 2, p = 0.35; DO, χ^2 = 3.1, df = 2, p = 0.21; turbidity, χ^2 = 3.6, df = 2, p = 0.17; pH, χ^2 = 0.04, df = 2, p = 0.98; ORP, χ^2 = 0.1, df = 2, p = 0.91; temperature, χ^2 = 1.6, df = 2, p = 0.45). All five parameters were significantly influenced by sample date (Nitrates/nitrites, χ^2 = 11.1, df =

4, p = 0.02, DO, χ^2 = 174.5, df = 4, p < 0.0001; turbidity, χ^2 = 40.6, df = 4, p < 0.0001; pH, χ^2 = 233.9, df = 4, p < 0.0001; ORP, χ^2 = 1527.3, df = 4, p < 0.0001; temperature, χ^2 = 3.213.2, df = 4, p < 0.0001). Only dissolved oxygen was significantly influenced by the interaction between salamander treatment and date (χ^2 = 16.5, df = 8, p = 0.02). Nitrates/nitrites, turbidity, pH, ORP, and temperature were not significantly influenced by this interaction (Nitrates/nitrites, χ^2 = 10.4, df = 8, p = 0.23; turbidity, χ^2 = 12.9, df = 8, p = 0.11; pH, χ^2 = 4.7, df = 8, p = 0.8=78; ORP, χ^2 = 2.1, df = 8, p = 0.97; temperature, χ^2 = 2.3, df = 8, p = 0.97).

DISCUSSION

Predation has a fundamental role in shaping ecological communities (Sih et al. 1985). Top-down control triggers trophic cascades, altering the abundances and species compositions of many trophic levels (Estes et al. 2011). However, the strength of top-down control can vary widely both among and within different ecosystems (Shurin and Borer 2002). A growing body of work has sought to understand the factors that alter top-down control strength (Borer et al. 2005). Body size variation among predators has implications for niche width (Woodward and Hildrew 2002), alterations of indirect interactions (Krenek and Rudolf 2014) and is a potential source of variation affecting top-down control (Ingram et al. 2011, Rudolf and Rasmussen 2013a). Here, we report on a mesocosm experiment in which we manipulated body size variation of salamanders and measured their effects on multiple trophic levels. While several studies have explored effects of body size variation in the context of trophic cascades (Simonis 2013, Geraldi 2015, Carlson and Langkilde 2017), few have manipulated predator body size variation while collecting as comprehensive a view of predator effects as this study (but see Blaustein, Friedman, & Fahima, 1996).

In our study, salamander predation affected nearly every measured component of the mesocosm communities, with top-down effects influencing populations at all trophic levels, from vertebrate consumers to invertebrate predators to primary producers. This corroborates with previous studies showing that salamanders can be effective predators in aquatic ecosystems (Dodson 1974, Morin et al. 1983, Blaustein et al. 1996, Wissinger et al. 1999, Rowland et al. 2017). Indeed, top down control was pervasive enough that we

found evidence for two trophic cascades triggered by salamanders, one through tadpoles on periphyton and the other through invertebrate predators on invertebrate collectors, each of which is discussed below (Figures 1 and 3). Overall, our hypothesis of strong-top down control by salamanders was supported.

While the majority of the biological communities responded to salamander presence, our hypotheses regarding body-size variation effects on strength of top-down control were not as well supported, with only a small subset of taxa showing responses to the different size-variation treatments, and neither of the detected trophic cascades were size-dependent. Specifically, only four measured variables were significantly different among all three salamander treatments; zooplankton abundances**,** Chironomid abundances from the benthic cores, and Ostracoda and Physidae abundances from the leaf packs. Of these four taxa, only Physidae snails had significantly greater abundances in High than Low treatments but abundances in the Control were still higher than in both salamander-present treatments. Zooplankton, Chironomids, and Ostracoda were all significantly less abundant in the High treatments than in the Low size variation treatments.

These results indicate that invertebrate taxa may have been more effectively suppressed in treatments with High size variation, contrary to our predictions of a stronger degree of suppression in Low size variation treatments. Some theory suggests that predator size variation increases niche breadth and may subsequently dampen trophic cascades due to weaker predation on any one prey type (Bolnick et al. 2011). However, the stronger effects in the High size variation mesocosms suggest that treatments with a variety of predator sizes had both a broader overall niche *and* stronger control of each of

their prey items than Low size variation treatments. While the lack of size class effect for many taxa suggests that niches were similarly broad among salamander treatments, the presence of a somewhat stronger effect in High than Low size variation treatments indicates that increased body size variation resulted in stronger top-down control. Such control could arise either through effective individual specialization (sensu Bolnick et al. 2003) of large and small salamanders on large and small prey respectively or due to extremely effective predation of all prey types by the largest salamander in the High tanks.

Size-dependent specialization, the former possibility, is quite likely since salamanders are gape-limited and experience size-dependent ontogenetic shifts (Holomuzki and Collins 1987, Taylor et al. 1988, Bardwell et al. 2007). Due to gape limitations, smaller salamanders are constrained to smaller prey, while larger salamanders often focus on the largest available prey (Wissinger et al. 1999, Johnson et al. 2003, Whiteman et al. 2003). Each size class of salamander would then exert strong predation pressure within their respective, more contracted niches. Thus, increased size variation creates a predator population with a broad overall niche composed of strongly interacting specialists. Ontogenetic stage-structure, often strongly linked to size-structure, has also been shown to lead to generalist populations composed of niche specialists (Rudolf and Lafferty 2011). Our results highlight the role that increased size variation plays in structuring communities.

Only a handful of biotic parameters in the mesocosms were not affected by salamander presence. Invertebrate predator abundances or biomasses from the benthic samples were not significantly different among salamander treatments. Additionally, total

biomasses of invertebrates from the benthos and biomasses of predators from leaf packs were not significantly affected by salamander treatment. Most of the abiotic water quality parameters (turbidity, pH, ORP, temperature, DO, and nitrate/nitrites) did not appear to have effects on or be affected by food web dynamics triggered by salamanders.

Benthic vs Leaf Pack Sampling

Variation in the effect of salamanders on invertebrate predator abundances and total invertebrate biomasses between the benthic and the leaf pack samples underscores the potential sampling differences of these two methods. Despite a high (Jaccard index of 89%) invertebrate community similarity between the leaf packs and the benthos, there was a striking difference in the effectiveness of the two methods in sampling Oligochaeta and Ostracoda. No Oligochaeta were found in the leaf packs, despite numbering in the hundreds in benthic samples. Conversely, very few Ostracoda were observed in the benthic samples despite reaching abundances into the thousands in leaf packs. It is not clear if this difference stems from an inherent tendency of a particular method to under-sample Oligochaetes or Ostracods, from differences in preservation (i.e., freezing the leaf packs vs. preserving the benthos in formalin), or from a potential refuge effect.

Data from the benthic core samples may be less reliable than from the leaf packs. Despite modifications, the benthic core sampler did not consistently seal with the bottom of the mesocosms, sometimes allowing part of the sample (and invertebrates) to escape. Additionally, the relatively qualitative collection of benthos from within the core might have led to an increased degree of variability among samples.

Another difference between the two methods may be that the leaf packs functioned as refuges from predation (Reice 1991), especially because the mesh of the leaf packs was sufficiently small to exclude all salamander sizes used in this experiment (R. Baker, personal observation). Yet, others have found no refuge effect of leaf packs when exposed to fish predators (Ruetz et al. 2002). Odonates and other invertebrate predators were apparently able to infiltrate the leaf packs since we frequently found them in our leaf pack samples. It is possible that the mesh may have excluded larger Odonates, but the largest Odonate found in the leaf packs was the same size as the largest Odonate found in the benthic samples (both 22 mm), suggesting little size-selective differences between benthos and leaf packs. In our results, predator and grazer abundances were comparable between leaf packs and benthos and trends of salamander treatment effects were similar across both sampling methods for most invertebrate responses. Thus, we assumed that there was no refuge effect and that leaf packs were a representative sample of the invertebrate community. Because of the issues described above with benthic cores, we primarily rely on data from the leaf pack invertebrate community to support the rest of our discussion.

Salamanders

Differences in body size variation among the predator populations were not as influential as simple predator presence/absence. The lack of a stronger size-variation effect could be due to the loss of salamanders over time, which altered the densities and size variation of salamanders in mesocosms. Although we maintained populations and size variation by replacing predators for the first month of the experiment, salamanders

continued to be lost via metamorphosis or death through the duration of the experiment. By the conclusion of the experiment, 36 out of an original 72 salamanders had been lost. Four of 36 mesocosms no longer had any salamanders left and only four mesocosms retained all three salamanders (Supplemental Figure 1). Changing predator densities can alter the amount of top-down predation experienced in the mesocosms if remaining salamanders cannot compensate for the loss of other predators. However, population declines due to metamorphosis are not unique to our experimental system; this is a natural process that commonly occurs in *A. talpoideum* populations (Whiteman 1994, Doyle and Whiteman 2008). Thus, the changes in densities are a realistic phenomenon that might help shed light on dynamics occurring in natural ponds.

Initially, there was a discrepancy in salamanders lost between size variation treatments while we replaced salamanders in the first month of the experiment, which might be related to the initial size of individual salamanders (Doyle and Whiteman 2008, Doyle et al. 2010). During the replacement period, nearly three-quarters of the 32 salamanders lost were from Low size treatment mesocosms and were all ‘medium’ sized salamanders. The remaining 9 salamanders lost from the High treatment were either ‘large’ or ‘medium’ salamanders. While this could indicate a propensity of larger salamanders to metamorphose, these results are biased by our ability to detect metamorphosing salamanders or deaths. Any direct consumption, such as by a large salamander eating a small salamander could not be confirmed by simple visual observations. However, at the end of the experiment, overall loss of salamanders was nearly evenly distributed between the two treatments, with 17 salamanders remaining in mesocosms with a High size variation treatment and 19 remaining in Low treatment

mesocosms. Due to the unreliability of grown-out or healed toe clips we were unable to identify individuals and provide information on survival rates based on salamanders' original sizes.

Loss of salamanders also reduced the differences in body size variation between treatments. Although the initial variation was significantly different between the High and Low treatments, between metamorphosing salamanders and growth of remaining salamanders, differences in body size variation among treatments decreased. By the end of the experiment, there was no significant difference between either the mean body sizes or the variation of salamander populations in tanks between High and Low treatments, eliminating the potential for late-experiment size-variation effects. Indeed, abundances of many taxa converged among all treatments by September. This could also be due to natural life-cycle dynamics of invertebrates as the season enters into fall. Additionally, trends between size variation treatments were fairly consistent over time for many taxa, suggesting that reduced densities of salamanders may not have influenced the differences in the size variation treatments. Yet, taken together, this highlights the temporal nature of community interactions and emphasizes that timing or season should be taken into account when examining trophic cascades (Howeth and Leibold 2008). In our experimental pond system, cascades were clearest during the early months (i.e. May and June) when the community was most productive and when both amphibian prey (tadpoles) and predators (salamanders) were at their highest abundances.

Despite any complicating factors of changing densities or body size variation, both presence and size class treatments of salamanders still had strong effects across many trophic levels in this experiment. This underscores the pervasiveness of

salamanders' top-down control. Even though predator densities and body size variation changed during the experiments, it still led to differences in several taxa, with High variation having a stronger effect than Low variation. This indicates that initial predator body size variation can strongly impact community organization, regardless of any temporal variation in predator populations.

Tadpoles, Snails, and Periphyton

Tadpoles are a strong interactor in aquatic systems, acting as voracious grazers and contributing to nutrient fluxes via feces (Seale 1980, Altig et al. 2007, Schiesari et al. 2009, Iwai et al. 2012). We observed significantly fewer tadpoles in tanks with salamanders than in tanks without salamanders. Tadpole abundances in all treatments decreased as tadpoles metamorphosed and left the mesocosms though the summer (Figure 1B).

Salamanders are common predators of eggs and tadpoles of many frog species (Morin 1983) and can also have indirect impacts on tadpole populations. For instance, Shaffery & Relyea (2016) demonstrated that gray tree frog tadpoles (*Hyla versicolor*) will reduce foraging and activity when exposed to chemical predator cues. Presence of salamander predators can also affect oviposition site choice of female Cope's gray tree frogs (*Hyla chrysoscelis*), with female frogs preferring to lay eggs in ponds without salamander predators (Resetarits and Wilbur 1989). Differences in tadpole abundances may have been due to direct consumption of eggs and larvae by predators, behavioral fear responses by tadpoles, selective oviposition by female frogs, or some combination of the above.

Salamanders affected populations of other grazers, especially Physidae snails (Figure 1C). In both leaf pack and benthic samples, Physidae abundances were significantly lower in the salamander-present treatments than in the Control treatment. In the leaf pack population, Physidae snails were additionally significantly lower in the Low treatment than in the High size variation treatment. Salamanders likely directly consumed the snails, which suppressed snail abundances in the salamander-present treatments and released snails from predation in the salamander-absent treatments. Additionally, the lower abundances of snails in the leaf packs from Low treatment might indicate a possible dietary preference of medium-sized salamanders for snails. For at least the snail population, these results support our initial hypothesis of stronger top-down control in lower size variation populations.

Periphyton biomass was significantly affected by both tadpoles and the interaction between salamander treatment and date. In the early months (May and June) periphyton was significantly lower in the Control treatment but towards the end of the experiment (in July and September) periphyton levels were the same among all treatments (Figure 1D). The convergence of periphyton biomasses among treatments in the later months is concurrent with the departure of tadpoles. Salamanders likely triggered a trophic cascade by suppressing tadpole abundances in the High and Low treatments that released periphyton from grazing pressure, but only in the first two months when tadpoles were most abundant. As tadpole abundances in all tanks reached similarly low densities, grazing pressure decreased, and periphyton biomasses in all treatments converged.

Lack of any differences of periphyton among treatments after most of the tadpoles had left indicates that snails did not have the same degree of herbivorous control that

tadpoles did, highlighting the strong role that tadpoles played in this ecosystem. Despite a top-down effect of salamanders on both snails and tadpoles, differences in the strength of the grazer-periphyton link led to differences in the existence of a trophic cascade. As demonstrated here, a strong consumer-resource link is essential to the propagation of a trophic cascade (DeLong et al. 2015)

Additionally, the lack of any significant main effects of salamander treatment or sample date indicates that periphyton concentration means were so similar, and variability around these means were so high in the later months, that it obscured the significant effects early in the experiment. Again, the existence of this trophic cascade in only half of our sample dates underscores the temporally dynamic nature of ecosystems (Howeth and Leibold 2008), particularly pond ecosystems that experience mass influxes and effluxes of amphibians and invertebrates over a season (Regester et al. 2006).

Invertebrate Predators and Collectors

Salamander presence significantly suppressed abundances of invertebrate predators in the leaf packs. In particular, Hydrophilidae larvae were the most abundant predator taxon observed and also had the strongest response to salamander treatments (Figure 3B). In contrast, invertebrate collector abundances and biomasses were significantly higher in the salamander-present treatments. Chironomidae larvae drove trends in the collector functional feeding group and are a common prey item for a diverse range of predators including salamanders and invertebrate predators (Taylor et al. 1988). However, more abundant Chironomids in the salamander-present treatments indicates any direct consumption by salamanders was not strong enough to control collectors.

Instead, collectors, particularly the Chironomid larvae, were most likely suppressed by invertebrate predators, especially the Hydrophilidae (Figure 3C). When salamanders were present, they controlled invertebrate predators, which in turn released the collectors from predation via a mesopredator release (Soule et al. 1988, Prugh et al. 2009). Classic examples of mesopredators often involve vertebrates, especially terrestrial mammals. The trophic cascade presented here demonstrates that freshwater invertebrates can be effective mesopredators, even with a vertebrate top predator.

Zooplankton and Phytoplankton

Salamander presence was correlated with changes in many other components of the food web, including zooplankton abundances and phytoplankton concentration, without necessarily causing a trophic cascade. Zooplankton models indicated a significant effect of salamander treatment but showed complex interactions among salamander treatments and date that were more easily deciphered by exploring the constituent taxa (Supplemental Figure 4). There are a number of potential explanations for these complex dynamics, since zooplankton populations are regulated by both bottom-up and top-down effects that could either cancel each other out or contribute to variable signals.

Alterations in the palatability or abundance of phytoplankton (by a competitor such as tadpoles) change zooplankton population dynamics (Bronmark et al. 1991, McCauley et al. 1999). The increased abundances of tadpoles and other herbivores in salamander-absent treatments along with higher Cladoceran abundances in the

salamander-present treatments could suggest that salamander suppression of larger herbivores may have released Cladocerans from competition for phytoplankton prey.

Additionally, top-down control of zooplankton has been observed in many other systems (e.g. Simonis, 2013; Stibor et al., 2004) and these increases in Cladocera abundances might also suggest a facilitative effect of salamanders via consumption of an intermediate predator, similar to the invertebrate predator-invertebrate collector dynamic described previously. While any cascade on zooplankton via an intermediate predator may have been dampened by salamanders' direct consumption (Taylor et al. 1988, Polis 1994), it is likely that salamanders preferentially preyed on larger food items (such as chironomids or tadpoles) given the large size discrepancy between zooplankton and salamanders in this system (Taylor et al. 1988, Whiteman et al. 2003, Bardwell et al. 2007).

Phytoplankton were also significantly influenced by salamander treatment, but this result was primarily driven by two sharp increases in concentration in the High treatment in May and July with no significant differences among the rest of the salamander*date interactions. Some of the obvious suspects in regulating phytoplankton populations, such as planktivorous zooplankton and tadpoles, and sun-blocking bladderwort mats did not directly correlate with the observed trends in phytoplankton.

While a decrease in phytoplankton in June does correlate with a peak in abundances of Cladocerans, indicating potential herbivorous control by these taxa, the phytoplankton trends are only in the High size variation treatment, while Cladocera abundances are similar in both High and Low treatments. Similarly, tadpole abundances

between High and Low treatments were not different, and could not explain the higher degree of variability in the High treatment of phytoplankton.

Conclusion

This study examined multiple facets of an experimental ecosystem to obtain a broad picture of predator effects on community structure and ecosystem function. The results demonstrate the pervasiveness of predator top-down control, and to a lesser degree, the importance of predator size structure on communities. When predator size variation mattered, a greater degree of body size variation generally led to stronger top-down control, perhaps due to individual specialization by differently sized salamanders. Overall predation by salamanders triggered multiple trophic cascades, illustrating the broad impacts of predation on aquatic food webs.

While we have compartmentalized and discussed the different aspects of this experimental ecosystem into more manageable chains (e.g. salamanders → tadpoles → periphyton or salamanders → invertebrate predators → invertebrate consumers), it is important to note that none of these food chains exist in isolation. Feedback cycles among all abiotic and biotic levels in the food web can link both ‘green’ (i.e. plant-based) channels and ‘brown’ (i.e. detritus based) channels (Iwai and Kagaya 2007, Sitvarin et al. 2016). Yet, this study still shows the strong effect of a predator across multiple different trophic levels and in several different food chains in one web, acting as a multichannel predator (Wolkovich et al., 2014). Whether a true trophic cascade is triggered, or is dampened due to complex interactions of intraguild predation, indirect interactions, compensatory dynamics, or other process, this study underscores the pervasiveness of

predator effects, an especially timely message as predators continue to be extirpated across ecosystems worldwide (Estes et al. 2011).

TABLES & FIGURES

Table 1. Mean snout vent length (SVL) and mean standard deviation of SVL within each trio of salamanders in the two salamander-present treatments. The High size variation treatment received one large, one small, and one medium salamander, while the Low size variation treatment received three medium salamanders.

	High Variation	Low Variation	*t*- value	df	*P*-value
Mean SVL (mm)	45.8 ±0.8	46.4 ±0.8	-1.965	21.9	0.062
Standard Deviation	16.1 ±1.3	5.3 ±1.6	19.97	21.0	**<0.0001**

Table 2. Results of generalized linear mixed models for invertebrates from the leaf pack and benthic samples as grouped by their overall abundances and biomasses, as well as abundances and biomasses of each functional feeding group. Significance and relative abundances of each salamander treatment (C = Control, L = Low, H = High) are shown when overall salamander treatment effect was significant. A comma between treatments means there was no significant difference and a > indicates a significant difference. For example, 'C, L > H' shows that there was no significant difference of a response variable between Control and Low treatments, but that Control and Low treatments were both higher than the High treatment.

Response	Predictors	χ^2	df	P-value	Salamander Treatments
Leaf Pack Abundances					
Total Abundance	Salamander Treatment	305.68	2	**<0.0001**	C, L > H
	Date	600.18	3	**<0.0001**	
	Sal Trt x Date	1168.41	6	**<0.0001**	
Total Abundance (without Ostracods)	Salamander Treatment	251.59	2	**<0.0001**	H, L > C
	Date	367.14	3	**<0.0001**	
	Sal Trt x Date	62.12	6	**<0.0001**	
Predators	Salamander Treatment	15.60	2	**0.0004**	C > H, L
	Date	60.54	3	**<0.0001**	
	Sal Trt x Date	19.17	6	**0.003**	
Collectors	Salamander Treatment	236.23	2	**<0.0001**	H, L > C
	Date	206.48	3	**<0.0001**	
	Sal Trt x Date	40.21	6	**<0.0001**	
	Hydrophilidae larvae	4.61	1	**0.03**	
Grazers	Salamander Treatment	60.64	2	**<0.0001**	H, L > C
	Date	782.38	3	**<0.0001**	
	Sal Trt x Date	93.31	6	**<0.0001**	
Filterers	Salamander Treatment	720.13	2	**<0.0001**	C > L > H
	Date	1257.84	3	**<0.0001**	
	Sal Trt x Date	1140.11	6	**<0.0001**	
Leaf Pack Biomasses					
Total Biomass	Salamander Treatment	6.19	2	**0.04**	C, L, H
	Date	21.79	3	**<0.0001**	
	Sal Trt x Date	6.18	6	0.40	
Total Biomass (without Ostracods)	Salamander Treatment	4.07	2	0.13	N/A
	Date	20.75	3	**0.0001**	
	Sal Trt x Date	3.18	6	0.79	
Predators	Salamander Treatment	3.76	2	0.15	N/A
	Date	20.75	3	**0.0001**	
	Sal Trt x Date	4.87	6	0.56	
Collectors	Salamander Treatment	25.08	2	<**0.0001**	C > H, L
	Date	30.38	3	<**0.0001**	
	Sal Trt x Date	3.69	6	0.71	
Grazers	Salamander Treatment	8.55	2	**0.01**	C, L, H
	Date	22.93	3	<**0.0001**	
	Sal Trt x Date	4.15	6	0.65	
Filterers	Salamander Treatment	8.82	2	**0.01**	C, L, H
	Date	12.18	3	**0.006**	
	Sal Trt x Date	10.15	6	0.11	
Benthic Abundances					
Total Abundances	Salamander Treatment	870.87	2	<**0.0001**	L, H > C
	Date	5499.95	4	<**0.0001**	
	Sal Trt x Date	218.36	8	<**0.0001**	
Predator	Salamander Treatment	1.21	2	0.54	N/A
	Date	412.94	4	<**0.0001**	
	Sal Trt x Date	3.90	8	0.86	
Collector	Salamander Treatment	1000.66	2	**<0.0001**	L, H > C
	Date	5168.31	4	**<0.0001**	
	Sal Trt x Date	358.33	8	**<0.0001**	
	Hydrophilidae larvae	554.42	1	**<0.0001**	
Grazer	Salamander Treatment	114.11	2	<**0.0001**	H > C
	Date	649.10	4	<**0.0001**	
	Sal Trt x Date	201.43	8	<**0.0001**	
Benthic Biomasses					
Total Biomass	Salamander Treatment	0.68	2	0.70	N/A
	Date	42.44	4	<**0.0001**	
	Sal Trt x Date	9.61	8	0.29	
Predators	Salamander Treatment	4.17	2	0.12	N/A
	Date	31.02	4	<**0.0001**	
	Sal Trt x Date	9.82	8	0.27	
Collectors	Salamander Treatment	9.01	2	**0.01**	H, L, C
	Date	68.32	4	<**0.0001**	
	Sal Trt x Date	4.02	8	0.85	
Grazers	Salamander Treatment	2.37	2	0.30	N/A
	Date	5.79	4	0.21	
	Sal Trt x Date	5.68	8	0.68	

Table 3. Results of generalized linear mixed models for tadpoles, primary producers, and zooplankton. All sample dates of tadpoles were used in the model presented below. Significance and relative abundances of each salamander treatment (C = Control, L = Low, H = High) are shown when overall salamander treatment effect was significant. A comma between treatments means there was no significant difference and a > indicates a significant difference. For example, 'C, L > H' shows that there was no significant difference of a response variable between Control and Low treatments, but that Control and Low treatments were both higher than the High treatment.

Response	Predictors	χ^2	df	P-value	Salamander Treatments
Tadpoles (All Dates)	Salamander Treatment	153.50	2	**<0.0001**	C > H, L
	Date	77.41	11	**<0.0001**	
	Sal Trt x Date	53.57	22	**0.0001**	
Phytoplankton	Salamander Treatment	15.48	2	**0.0004**	H > C
	Date	14.24	4	**0.006**	
	Sal Trt x Date	6.98	8	0.53	
Periphyton (All Dates)	Salamander Treatment	0.09	2	0.95	N/A
	Date	0.63	2	0.72	
	Sal Trt x Date	2.43	4	0.65	
	Physidae	0.004	1	0.94	
	Tadpoles	9.29	1	**0.002**	
Periphyton (May & June Only)	Salamander Treatment	9.98	2	**0.007**	C > H, L
	Date	0.0001	1	0.99	
	Sal Trt x Date	1.0	2	0.61	
Total Zooplankton	Salamander Treatment	50.69	2	**<0.0001**	L > C > H
	Date	499.52	4	**<0.0001**	
	Sal Trt x Date	109.707	8	**<0.0001**	
Cladocera	Salamander Treatment	22.11	2	**<0.0001**	L > C, H
	Date	376.86	4	**<0.0001**	
	Sal Trt x Date	43.25	8	**<0.0001**	
Copeopod	Salamander Treatment	42.05	2	**<0.0001**	L > C, H
	Date	369.73	4	**0.0001**	
	Sal Trt x Date	141.92	8	**0.0001**	
Nauplii	Salamander Treatment	54.76	2	**<0.0001**	L, C > H
	Date	781.09	4	**0.0001**	
	Sal Trt x Date	78.78	8	**0.0001**	
Rotifer	Salamander Treatment	6.41	2	**0.04**	C, L, H
	Date	237.92	4	**<0.0001**	
	Sal Trt x Date	22.97	8	**0.003**	

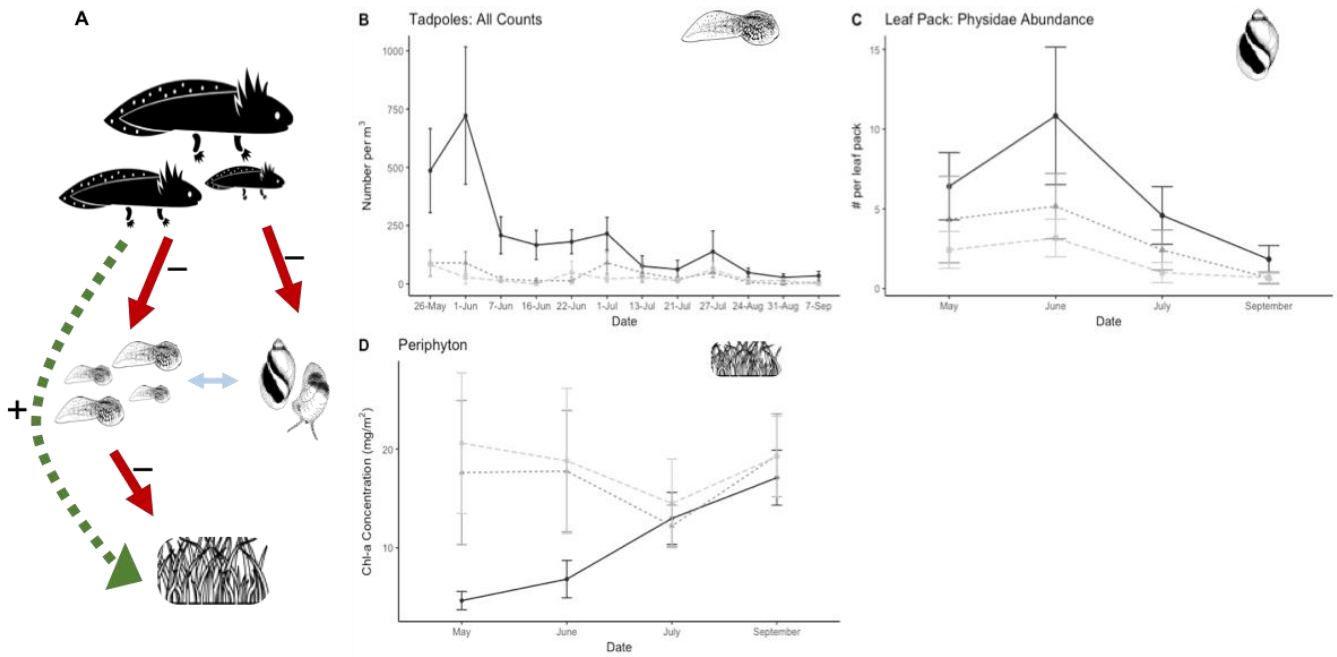

Figure 1. Food-chain depiction of a trophic cascade (A) initiated by salamanders on tadpoles and periphyton. Direct negative effects of a predator or consumer are indicated by solid red arrows, indirect positive effects by a dashed green arrow, and potential competition by a light blue double-headed arrow. Abundances of both tadpoles (B) and Physidae (C) were higher in the Control treatment (solid black line) than in either of the salamander-present treatments (dashed grey lines). Periphyton concentration (D) was lower in the earlier months of the Control treatment, commensurate with the high abundances of tadpoles at the same time.

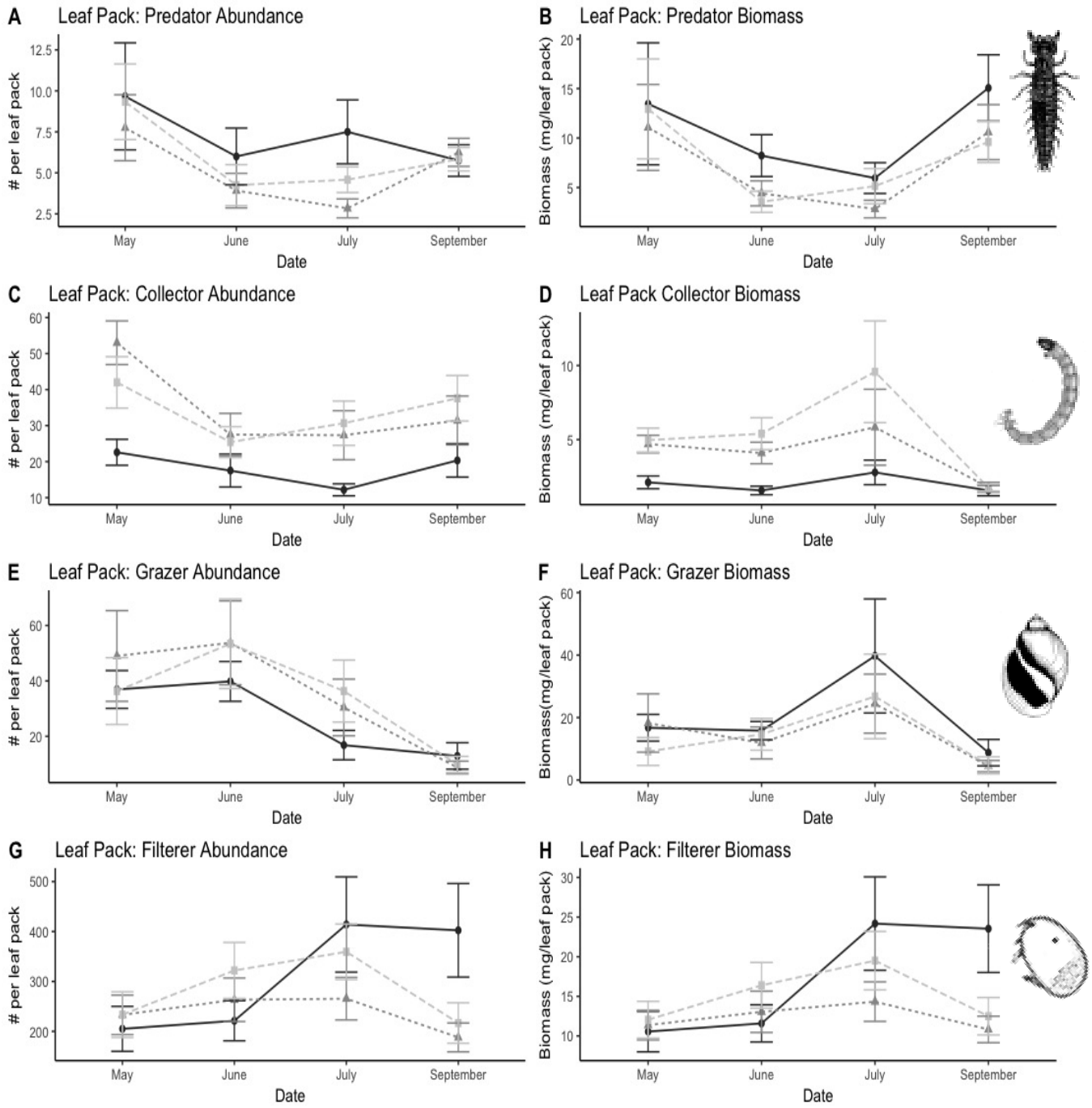

Figure 2. Mean ± SE of abundances and biomasses of invertebrates from the leaf packs grouped by four functional feeding groups. Panels on the left-hand side show abundances of predators (A), collectors (C), grazers (E) and filterers (G). Panels on the right hand side show biomasses of predators (B), collectors (D), grazers (F), and filterers (H). Control treatments are noted by a solid black line with circles, High size variation treatments by a dark grey dotted line with triangles, and Low size variation treatments by a light grey dashed line with squares.

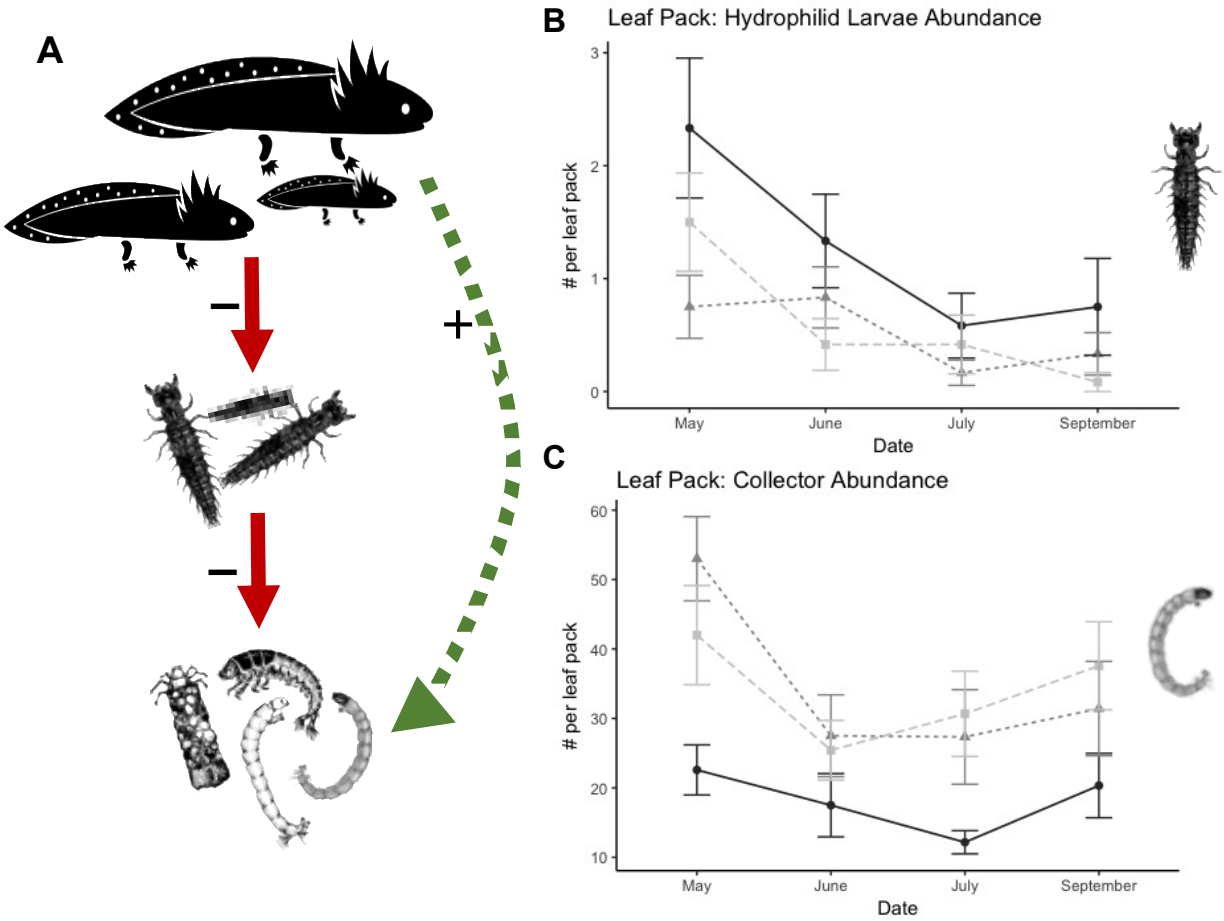

Figure 3. A food-chain visualization (A) of a trophic cascade initiated by salamanders on predatory Hydrophilidae beetle larvae and collectors, primarily composed of Chironomidae larvae. Abundances of Hydrophilidae (B) were higher in the Control treatments (solid black line) than in either of the salamander-present treatments (dashed grey lines). Conversely, collector abundances (C) were higher in both salamander-present treatments than in the Control treatments. This illustrates a potential trophic cascade in which salamanders suppressed invertebrate predator abundances which indirectly facilitated an increased abundance of collectors.

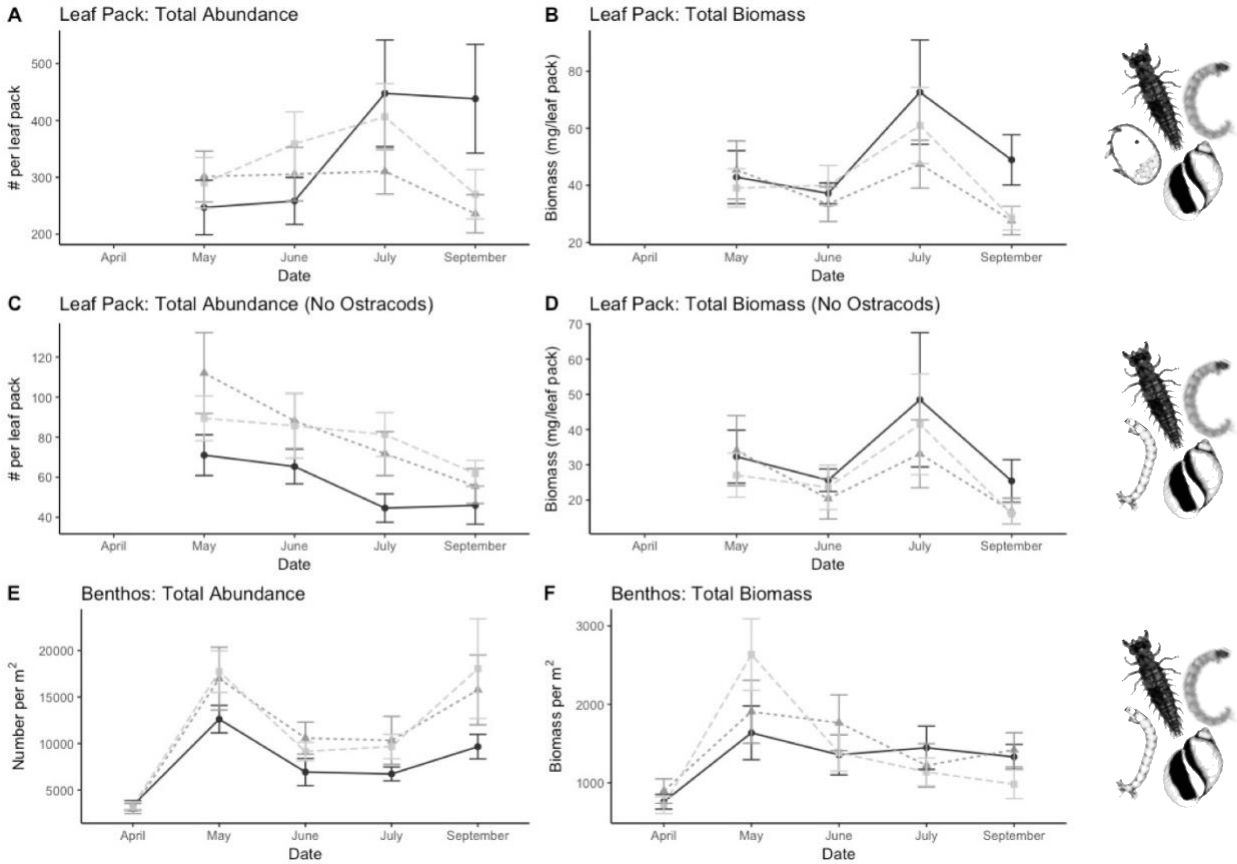

Figure 4. Total invertebrate abundances and biomasses from leaf pack and benthic samples. Panels A and B show leaf pack invertebrate abundances (A) and biomasses (B) with Ostracoda. Panels C and D show the leaf pack community abundances (C) and biomasses (D) without Ostracoda. Panels E and F show total abundances (E) and biomasses (F) of invertebrate from the benthic samples. Control treatments are noted by a solid black line with circles, High size variation treatments by a dark grey dotted line with triangles, and Low size variation treatments by a light grey dashed line with squares.

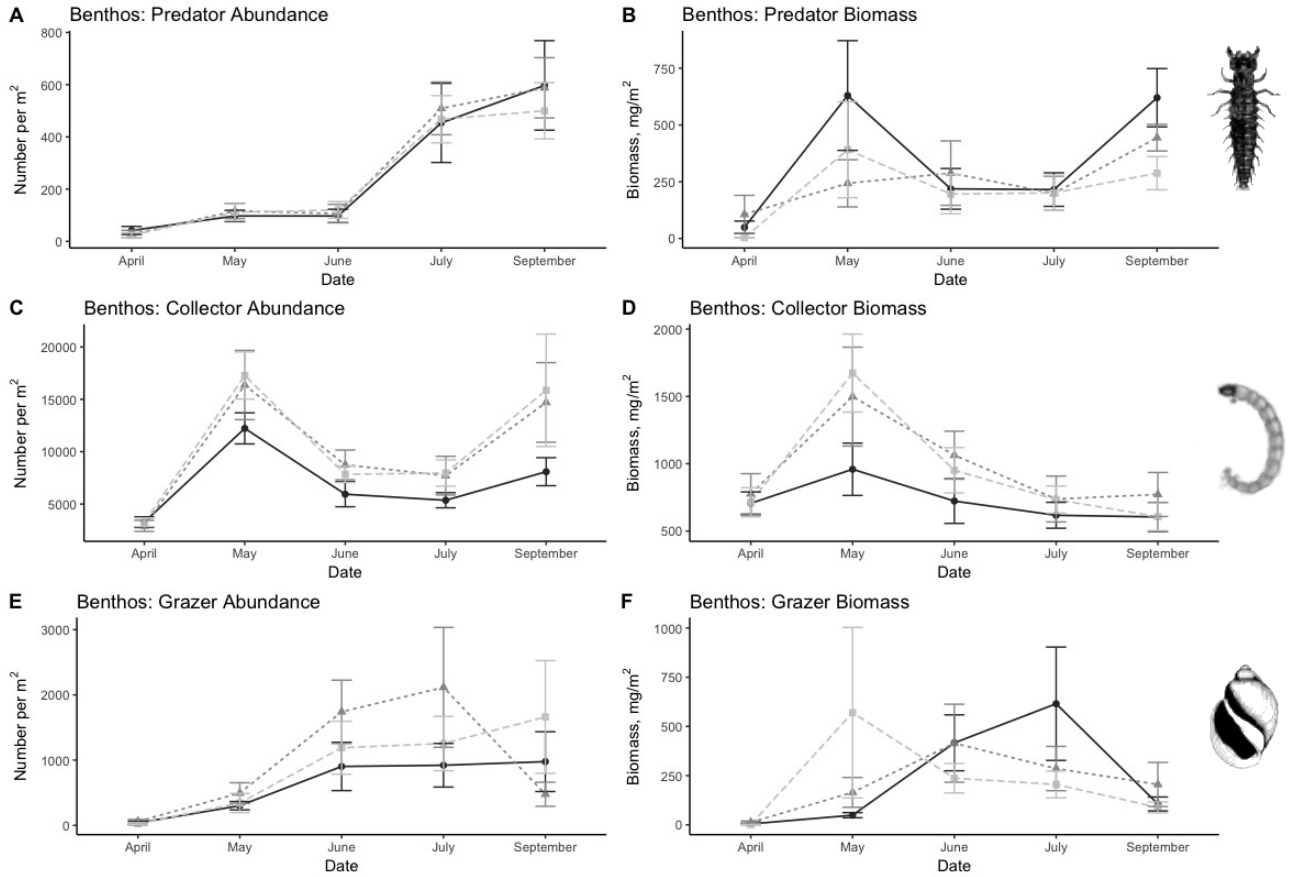

Figure 5. Mean ± SE of invertebrate abundances and biomass from the benthic samples, grouped by the three functional feeding groups present in this community. Panels on the left-hand side show abundances of predators (A), collectors (C), and grazers (E). Panels on the right hand side show biomasses of predators (B), collectors (D), and grazers (F). Filterers are not displayed because there were nearly no filterers in the benthic samples. Control treatments are noted by a solid black line with circles, High size variation treatments by a dark grey dotted line with triangles, and Low size variation treatments by a light grey dashed line with squares

SUPPLEMENTAL TABLES AND FIGURES

Table 1. Length-mass regressions and sources along with functional feeding groups based on Merritt and Cummins, 4th edition. In regression equations, 'm' is estimated biomass based on measured length, 'L'. Some taxa did not have specific length-mass regressions published, so we used regressions from a broader taxonomic resolution (e.g. we used a length mass regression for Odonata for both Anisoptera and Zygoptera). No regression equation could be found for Nematoda, so we used an equation for Oligochaeta because they have very similar body shapes.

Taxa	Length- Mass Regression	Length-Mass Source	Functional Feeding Group
Ancylidae	m=0.0087*L^3.21	(As Gastropod) Baumgartner & Rothhaupt 2003	Grazer
Anisoptera	m=0.0078*L^2.792	(As Odonate) Benke 1999	Predator
Ceratopogonidae	m=0.0025*L^2.469	Benke 1999	Predator
Chaoboridae	m=0.0025*L^2.692	(As Diptera) Benke 1999	Predator
Chironomidae	m=0.0018*L^2.617	Benke 1999	Collector
Culicidae	m=0.032*L^2.038	Sabo 2002	Collector
Dytiscidae	m=0.0077*L^2.91	(As Coleoptera) Benke 1999	Predator
Ephemeroptera	m=0.0071*L^2.832	Benke 1999	Collector
Hirudinea	m=0.081*L^1.919	A.J. Klemmer unpublished data	Predator
Hydrachnida	m=0.132*L^1.66	Baumgartner & Rothhaupt 2003	Predator
Hydrophilidae	m=0.0077*L^2.91	(As Coleoptera) Benke 1999	Predator
Lymnaeidae	m=0.0087*L^3.21	(As Gastropod) Baumgartner & Rothhaupt 2003	Grazer
Miscellaneous	N/A	N/A	N/A
Nematoda	m=0.0024*L^1.875	(As Oligochaete) Stoffels 2003	Collector
Oligochaete	m=0.0024*L^1.875	Stoffels 2003	Collector
Ostracoda	m=0.06	Own	Filterer
Physidae	m=0.0087*L^3.21	(As Gastropod) Baumgartner & Rothhaupt 2003	Grazer
Trichoptera	m=0.0056*L^2.839	Benke 1999	Collector
Zygoptera	m=0.0078*L^2.792	(As Odonate) Benke 1999	Predator

Table 2. Results of generalized linear mixed models for water parameters, bladderwort coverage, and decomposition. Significance and relative abundances of each salamander treatment (C = Control, L = Low, H = High) are shown when overall salamander treatment effect was significant. A comma between treatments means there was no significant difference and a > indicates a significant difference. For example, 'C, L > H' shows that there was no significant difference of a response variable between Control and Low treatments, but that Control and Low treatments were both higher than the High treatment.

Response	Predictors	χ^2	df	P-value	Salamander Treatments
Water Parameters					
Dissolved Oxygen	Salamander Treatment	3.33	2	0.18	N/A
	Date	189.86	4	**<0.00001**	
	Sal Trt x Date	17.96	8	**0.02**	
Turbidity	Salamander Treatment	3.60	2	0.16	N/A
	Date	40.63	4	**<0.00001**	
	Sal Trt x Date	12.90	8	0.11	
pH	Salamander Treatment	0.03	2	0.98	N/A
	Date	233.92	4	**<0.00001**	
	Sal Trt x Date	4.71	8	0.78	
ORP	Salamander Treatment	0.17	2	0.91	N/A
	Date	1527.33	4	**<0.00001**	
	Sal Trt x Date	2.14	8	0.97	
Temperature	Salamander Treatment	1.57	2	0.45	N/A
	Date	3213.2	4	**<0.00001**	
	Sal Trt x Date	2.3	8	0.97	
Conductivity	Salamander Treatment	13.17	2	**0.001**	L > H
	Date	518.89	4	**<0.00001**	
	Sal Trt x Date	1.44	8	0.99	
Nitrate/nitrites	Salamander Treatment	2.06	2	0.35	N/A
	Date	11.17	4	**0.02**	
	Sal Trt x Date	10.40	8	0.23	
SRP	Salamander Treatment	3.55	2	**0.008**	C, H, L
	Date	146.69	4	**<0.00001**	
	Sal Trt x Date	3.55	8	0.89	
Surface Area Coverage					
Bladdewort+Algae	Salamander Treatment	6.97	2	**0.03**	H > C
	Date	79.11	3	**<0.00001**	
	Sal Trt x Date	8.85	6	0.18	
Just Bladderwort	Salamander Treatment	4.38	2	0.11	N/A
	Date	90.11	3	**<0.00001**	
	Sal Trt x Date	11.43	6	0.07	
Just Algae	Salamander Treatment	2.58	2	0.27	N/A
	Date	16.17	3	**0.001**	
	Sal Trt x Date	5.40	6	0.49	
Decomposition					
% AFDM	Salamander Treatment	4.60	2	0.09	N/A
	Date	589.49	3	**<0.00001**	
	Sal Trt x Date	4.79	6	0.57	

Table 3. Results of generalized linear mixed models for the Simpson diversity index and abundances and biomasses of individual invertebrate taxa from the leaf packs. Significance and relative abundances of each salamander treatment (C = Control, L = Low, H = High) are shown when overall salamander treatment effect was significant. A comma between treatments means there was no significant difference and a > indicates a significant difference. For example, 'C, L > H' shows that there was no significant difference of a response variable between Control and Low treatments, but that Control and Low treatments were both higher than the High treatment.

Response	Predictors	χ^2	df	P-value	Salamander Treatment
Leaf Pack Abundances					
Anisoptera	Salamander Treatment	0.38	2	0.82	N/A
	Date	148.77	3	**<0.0001**	
	Sal Trt x Date	3.39	6	0.75	
Hydrophilidae	Salamander Treatment	20.76	2	**<0.0001**	C > H, L
	Date	41.71	3	**<0.0001**	
	Sal Trt x Date	6.03	6	0.41	
Ceratopogonidae	Salamander Treatment	7.24	2	**0.02**	L, C, H
	Date	137.19	3	**<0.0001**	
	Sal Trt x Date	18.08	6	**0.006**	
Chironomidae	Salamander Treatment	253.4	2	**<0.0001**	H, L > C
	Date	275.96	3	**<0.0001**	
	Sal Trt x Date	56.7	6	**<0.0001**	
	Hydrophilidae	5.12	1	**0.02**	
Trichoptera	Salamander Treatment	10.34	2	**0.005**	L, H, C
	Date	70.83	3	**<0.0001**	
	Sal Trt x Date	5.04	6	0.53	
Ancylidae	Salamander Treatment	105.32	2	**<0.0001**	L , H > C
	Date	131.33	3	**<0.0001**	
	Sal Trt x Date	5.09	6	0.53	
Physidae	Salamander Treatment	132.43	2	**<0.0001**	C > H > L
	Date	647.59	3	**<0.0001**	
	Sal Trt x Date	111.79	6	**<0.0001**	
Lymnaeidae	Salamander Treatment	2.77	2	0.24	N/A
	Date	13.15	3	**0.004**	
	Sal Trt x Date	13.55	6	**0.03**	
Simpson Diversity	Salamander Treatment	7.26	2	**0.02**	H > C
	Date	38.09	3	**<0.00001**	
	Sal Trt x Date	11.41	6	**0.07**	
Leaf Pack Biomasses					
Anisoptera	Salamander Treatment	0.97	2	0.61	N/A
	Date	12.42	3	**0.006**	
	Sal Trt x Date	1.02	6	0.98	
Hydrophilidae	Salamander Treatment	8.61	2	**0.01**	C, L, H
	Date	19.45	3	**0.0002**	
	Sal Trt x Date	4.71	6	0.58	
Ceratopogonidae	Salamander Treatment	3.73	2	0.15	N/A
	Date	35.56	3	**<0.0001**	
	Sal Trt x Date	3.67	6	0.72	
Chironomidae	Salamander Treatment	212.07	2	**<0.00001**	L, H > C
	Date	277.91	3	**<0.00001**	
	Sal Trt x Date	52.92	6	**<0.00001**	
Trichoptera	Hydrophilidae	5.12	1	**0.02**	C, H, L
	Date	90.56	3	**<0.0001**	
	Sal Trt x Date	8.09	6	0.23	
Physidae	Salamander Treatment	12.04	2	**0.002**	C > L
	Date	6.97	3	0.07	
	Sal Trt x Date	4.52	6	0.60	
Ancylidae	Salamander Treatment	1.68	2	0.43	N/A
	Date	55.73	3	**<0.0001**	
	Sal Trt x Date	5.46	6	0.48	

Table 4. Results of generalized linear mixed models for the Simpson diversity index and abundances and biomasses of individual invertebrate taxa from the benthos. Significance and relative abundances of each salamander treatment (C = Control, L = Low, H = High) are shown when overall salamander treatment effect was significant. A comma between treatments means there was no significant difference and a > indicates a significant difference. For example, 'C, L > H' shows that there was no significant difference of a response variable between Control and Low treatments, but that Control and Low treatments were both higher than the High treatment.

Response	Predictors	χ^2	df	P-value	Salamander Treatment
Benthos Abundances					
Anisoptera	Salamander Treatment	1.22	2	0.54	N/A
	Date	446.04	4	**<0.0001**	
	Sal Trt x Date	2.77	8	0.94	
Hydrophilidae	Salamander Treatment	5.97	2	**0.05**	C, H, L
	Date	9.70	4	**0.04**	
	Sal Trt x Date	3.76	8	0.87	
Chironomid	Salamander Treatment	275.59	2	**<0.0001**	L > H > C
	Date	1740.82	4	**<0.0001**	
	Sal Trt x Date	83.79	8	**<0.0001**	
	Hydrophilidae larvae	79.66	1	**<0.0001**	
Oligochaeta	Salamander Treatment	480.64	2	**<0.0001**	H, L > C
	Date	4720.11	4	**<0.0001**	
	Sal Trt x Date	198.26	8	**<0.0001**	
Trichoptera	Salamander Treatment	9.64	2	**0.008**	H, C, L
	Date	484.86	4	**<0.0001**	
	Sal Trt x Date	20.86	8	**0.007**	
Physidae	Salamander Treatment	10.47	2	**0.005**	C > L
	Date	44.49	4	**<0.0001**	
	Sal Trt x Date	7.5	8	0.48	
Ancylidae	Salamander Treatment	141.12	2	**<0.0001**	H, L > C
	Date	606.09	4	**<0.0001**	
	Sal Trt x Date	209.69	8	**<0.0001**	
Simpson Diversity	Salamander Treatment	1.49	2	0.47	N/A
	Date	20.03	4	**0.0004**	
	Sal Trt x Date	6.64	8	0.57	
Benthos Biomass					
Hydrophilidae	Salamander Treatment	9.33	2	**0.009**	L > C
	Date	21.66	4	**0.0002**	
	Sal Trt x Date	3.76	8	0.87	
Chironomid	Salamander Treatment	6.78	2	**0.03**	C > L
	Date	70.53	4	**<0.0001**	
	Sal Trt x Date	4.69	8	0.78	
Oligochaeta	Salamander Treatment	3.9	2	0.14	N/A
	Date	139.74	4	**<0.0001**	
	Sal Trt x Date	3.49	8	0.89	
Trichoptera	Salamander Treatment	4.85	2	0.08	N/A
	Date	89.86	4	**<0.0001**	
	Sal Trt x Date	11.56	8	0.17	
Physidae	Salamander Treatment	8.68	2	**0.01**	L, C, H
	Date	88.26	4	**<0.0001**	
	Sal Trt x Date	26.35	8	**0.0009**	
Ancylidae	Salamander Treatment	8.65	2	**0.01**	C, L, H
	Date	122.89	4	**<0.0001**	
	Sal Trt x Date	10.4	8	0.23	

Table 5. Model specifications for Generalized Linear Mixed Models conducted. Each response variable tested is shown with its best-fitting distribution family (and link, if used). Gaussian families with no link were run as a Linear Mixed Model (LMM). Any adjustments to response variables are noted, i.e. adding a constant or scaling the variable. Finally, changes to the model specification are noted, i.e. changing the standard Nelder-Mead optimizer or specifying starting values for the model. All analyses were conducted in R 3.3.1 using the 'glmer' function in the 'lme4' package.

Response Variable	Distribution Family/Link	Adjustments to response variable	Model Specifications
Biotic Parameters			
Tadpoles (full)	Poisson	N/A	N/A
Phytoplankton	Gaussian/Log	+ 1	bobyqa
Periphyton (all dates)	Gamma	N/A	bobyqa
Periphyton (May & June only)	Gamma	N/A	bobyqa
Total Zooplankton	Poisson	N/A	N/A
Cladocera	Poisson	+ 1	N/A
Copeopod	Poisson	N/A	N/A
Nauplii	Poisson	N/A	N/A
Rotifer	Poisson	+ 1	N/A
Water Parameters			
Dissolved Oxygen	Gaussian (LMM)	N/A	N/A
Turbidity	Gaussian/Log	+ 1	bobyqa
pH	Gaussian/Log	N/A	bobyqa
ORP	Gaussian (LMM)	N/A	N/A
Temperature	Gaussian (LMM)	N/A	N/A
Conductivity	Gamma	N/A	bobyqa
Nitrate/nitrites	Gaussian/Log	+ 0.01	bobyqa
SRP	Gaussian/Log	N/A	bobyqa
Surface Area Coverage			
Bladdewort+Algae	Gamma	+ 1000	bobyqa
Just Bladderwort	Gamma	+ 1000	bobyqa
Just Algae	Gaussian (LMM)	N/A	N/A
Decomposition			
% AFDM	Gaussian (LMM)	N/A	N/A

[Continues on next page]

[Table 5 continued]

Leaf Pack Abundances			
Total Abundance	Poisson	N/A	N/A
Total Abundance (without Ostracods)	Poisson	N/A	N/A
Predators	Poisson	N/A	N/A
Collectors	Poisson	N/A	bobyqa
Grazers	Poisson	N/A	N/A
Filterers	Poisson	N/A	N/A
Anisoptera	Poisson	+ 1	bobyqa
Hydrophilidae	Poisson	N/A	N/A
Ceratopogonidae	Poisson	N/A	N/A
Chironomidae	Poisson	N/A	N/A
Trichoptera	Poisson	N/A	bobyqa
Ancyclidae	Poisson	N/A	N/A
Physidae	Poisson	N/A	bobyqa
Lymnaeidae	Poisson	N/A	N/A
Simpson Diversity	Gaussian (LMM)	N/A	N/A
Leaf Pack Biomasses			
Total Biomass	Gaussian/Log	Scaled	bobyqa, specified starting values
Total Biomass (without Ostracods)	Gaussian/Log	Scaled	bobyqa, specified starting values
Predators	Gamma	+ 1	bobyqa
Collectors	Gamma	N/A	bobyqa
Grazers	Gaussian/Log	Scaled	bobyqa, specified starting values
Filterers	Gaussian/Log	Scaled	bobyqa, specified starting values
Anisoptera	Gaussian/Log	+ 1	bobyqa
Hydrophilidae	Gaussian/Log	+ 1	bobyqa
Ceratopogonidae	Gamma	+ 1	bobyqa
Chironomidae	Gaussian/Log	N/A	bobyqa
Trichoptera	Gamma	+ 1	bobyqa
Physidae	Gaussian/Log	+ 1	bobyqa
Ancyclidae	Gaussian/Log	+ 1	bobyqa
Benthic Abundances			
Total Abundances	Poisson	N/A	N/A
Predator	Poisson	N/A	bobyqa
Collector	Poisson	N/A	bobyqa
Grazer	Poisson	N/A	bobyqa
Anisoptera	Poisson	+ 1	bobyqa
Hydrophilid	Poisson	+ 1	bobyqa
Chironomid	Poisson	N/A	bobyqa
Oligochaeta	Poisson	N/A	bobyqa
Trichoptera	Poisson	N/A	bobyqa
Physidae	Poisson	+ 1	bobyqa
Ancyclidae	Poisson	N/A	bobyqa
Simpson Diversity	Gaussian (LMM)	N/A	N/A
Benthic Biomasses			
Total Biomass	Gamma	N/A	bobyqa
Predators	Gamma	+ 1	bobyqa
Collectors	Gaussian/Log	Scaled	bobyqa, specified starting values
Grazers	Gaussian/Log	Scaled, + 1	bobyqa, specified starting values
Hydrophilid	Gamma	+ 1	bobyqa
Chironomid	Gamma	N/A	bobyqa
Oligochaeta	Gamma	+ 1	bobyqa
Trichoptera	Gamma	+ 1	bobyqa
Physidae	Gamma	+ 1	bobyqa
Ancyclidae	Gamma	+ 1	bobyqa

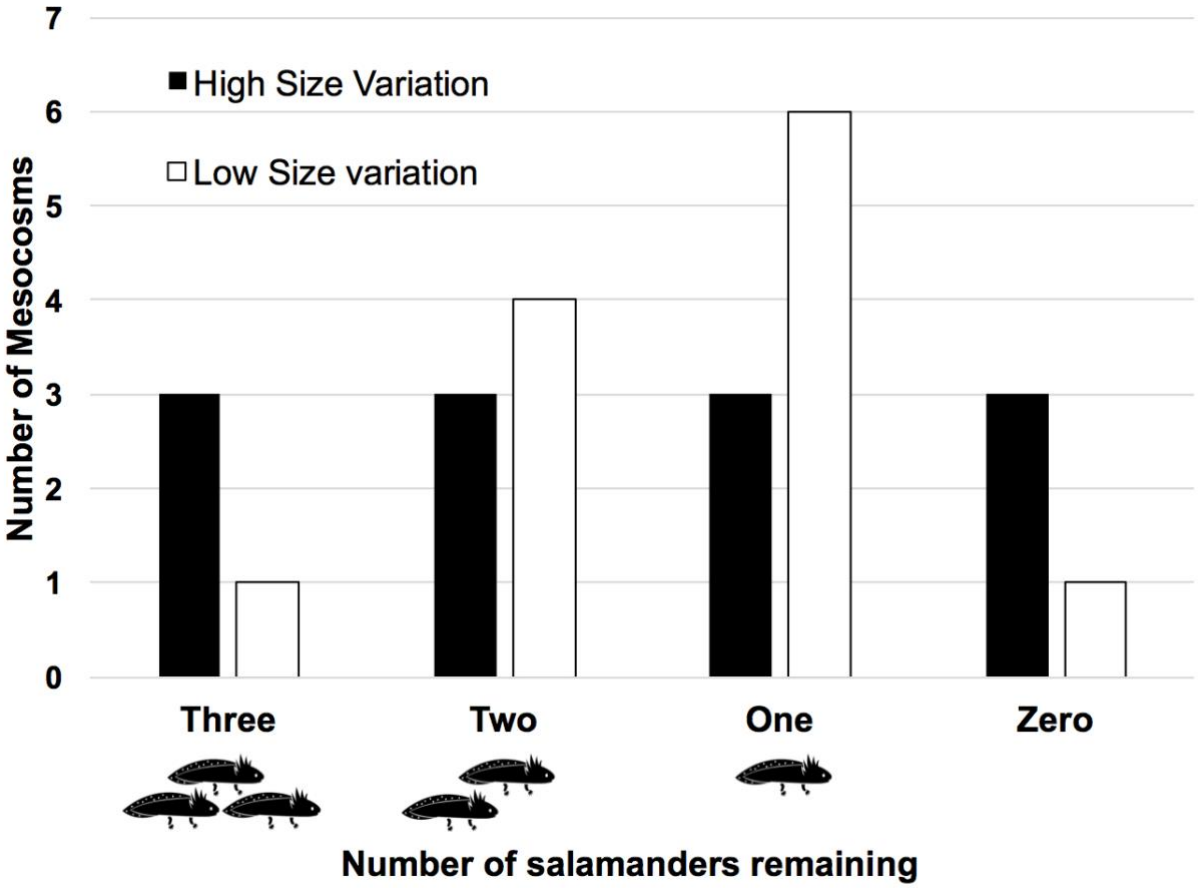

Figure 1. Number of mesocosms with three, two, one, or zero salamanders remaining at the conclusion of the experiment in each treatment.

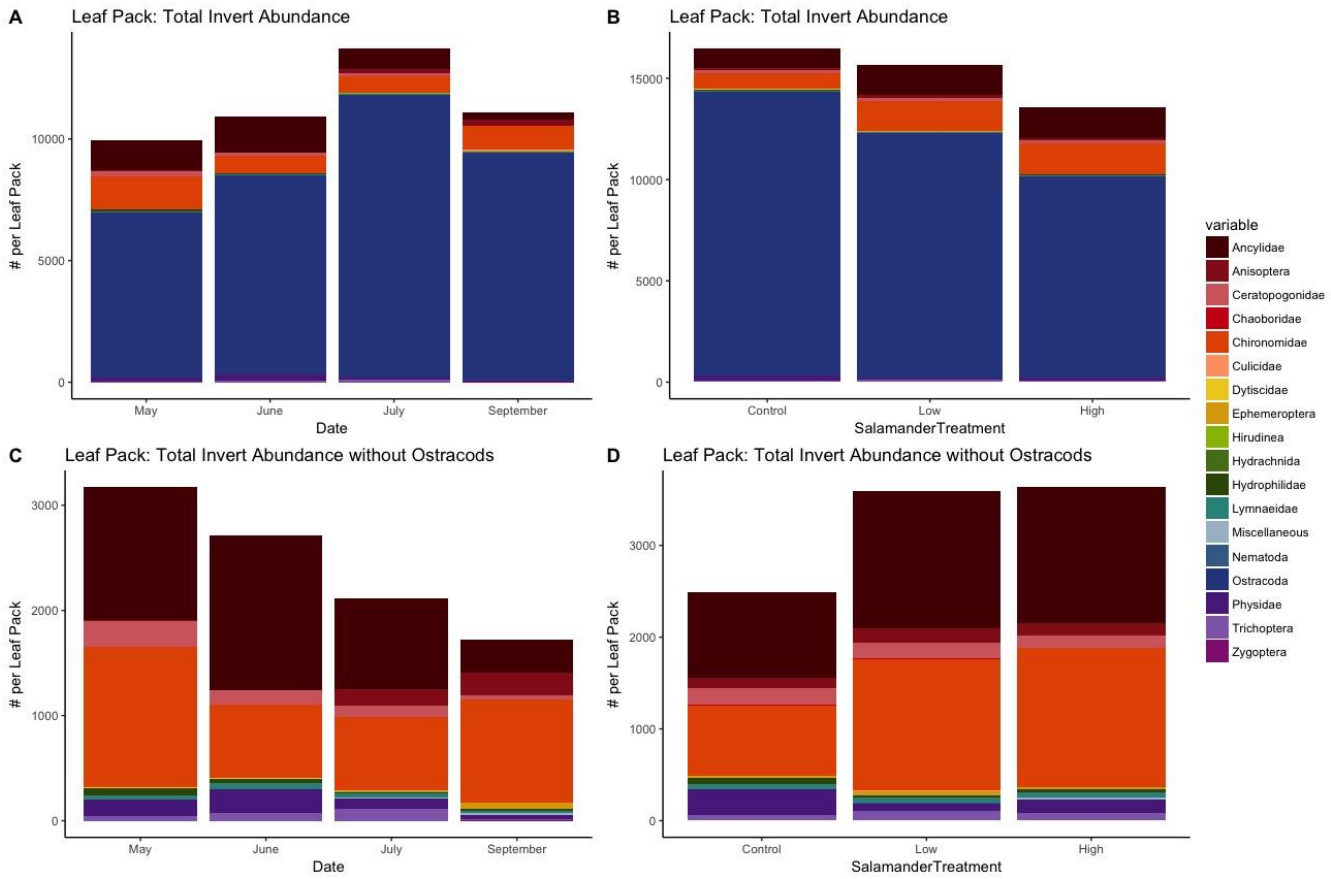

Figure 2. Composition of invertebrate communities based on invertebrate abundances from the leaf packs across sample date (Panels A and C) and salamander treatments (B and D). Ostracoda were by far the most abundant taxa (navy blue in panels A and B), and were removed in panels C and D to reveal trends among the remaining taxa.

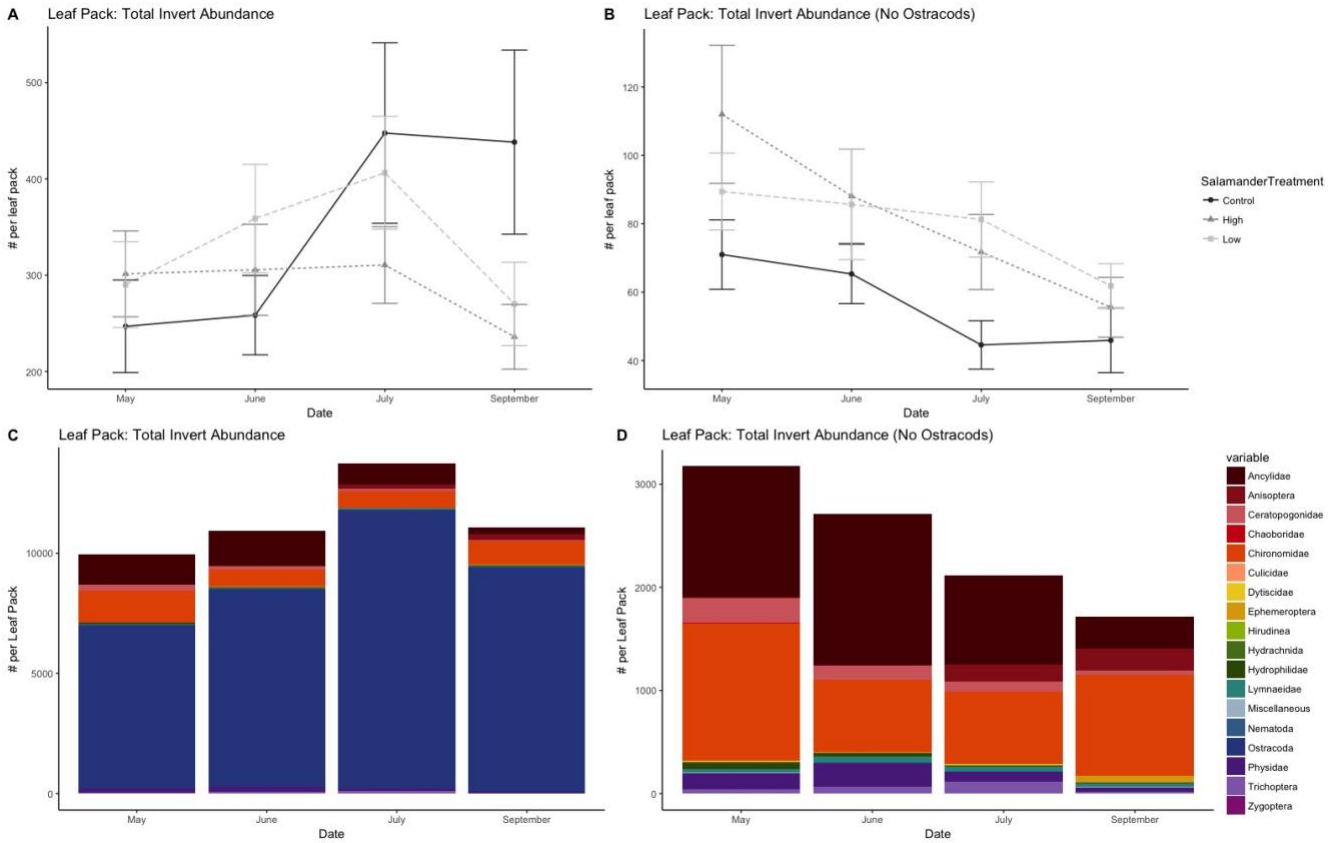

Figure 3. Mean ± SE of total invertebrate abundances (A, B) and invertebrate community Composition (C, D) with and without Ostracoda from the leaf packs. Panels A and C show abundances with Ostracoda, panels B and D show abundances without Ostracoda. In panels A and B, Control treatments are noted by a solid black line with circles, High size variation treatments by a dark grey dotted line with triangles, and Low size variation treatments by a light grey dashed line with squares.

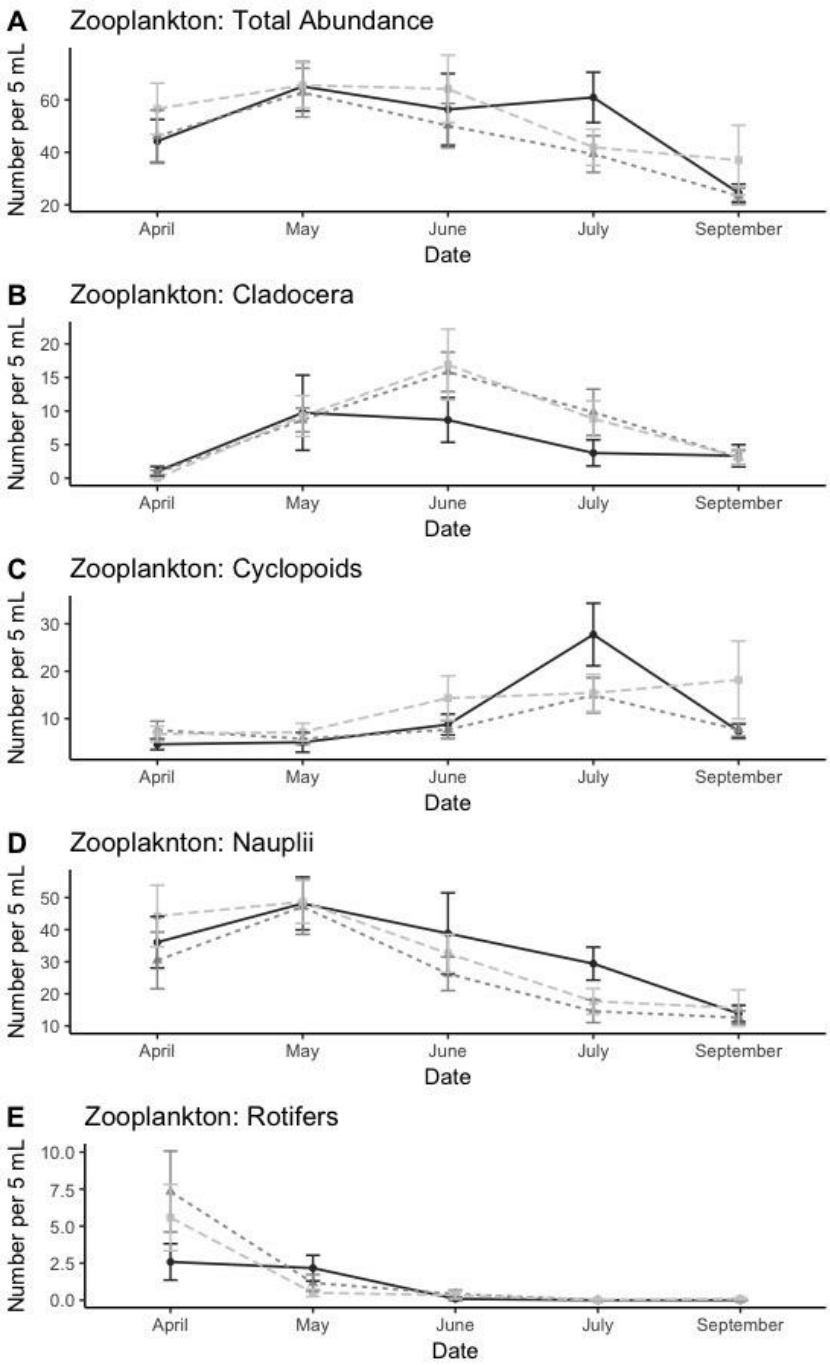

Figure 4. Mean ± SE abundances of total zooplankton (A), and the constituent zooplankton species: Cladocera (B), Copepoda (B), larval Copepods known as Nauplii (D), and Rotifers (E). Control treatments are noted by a solid black line with circles, High size variation treatments by a dark grey dotted line with triangles, and Low size variation treatments by a light grey dashed line with squares.

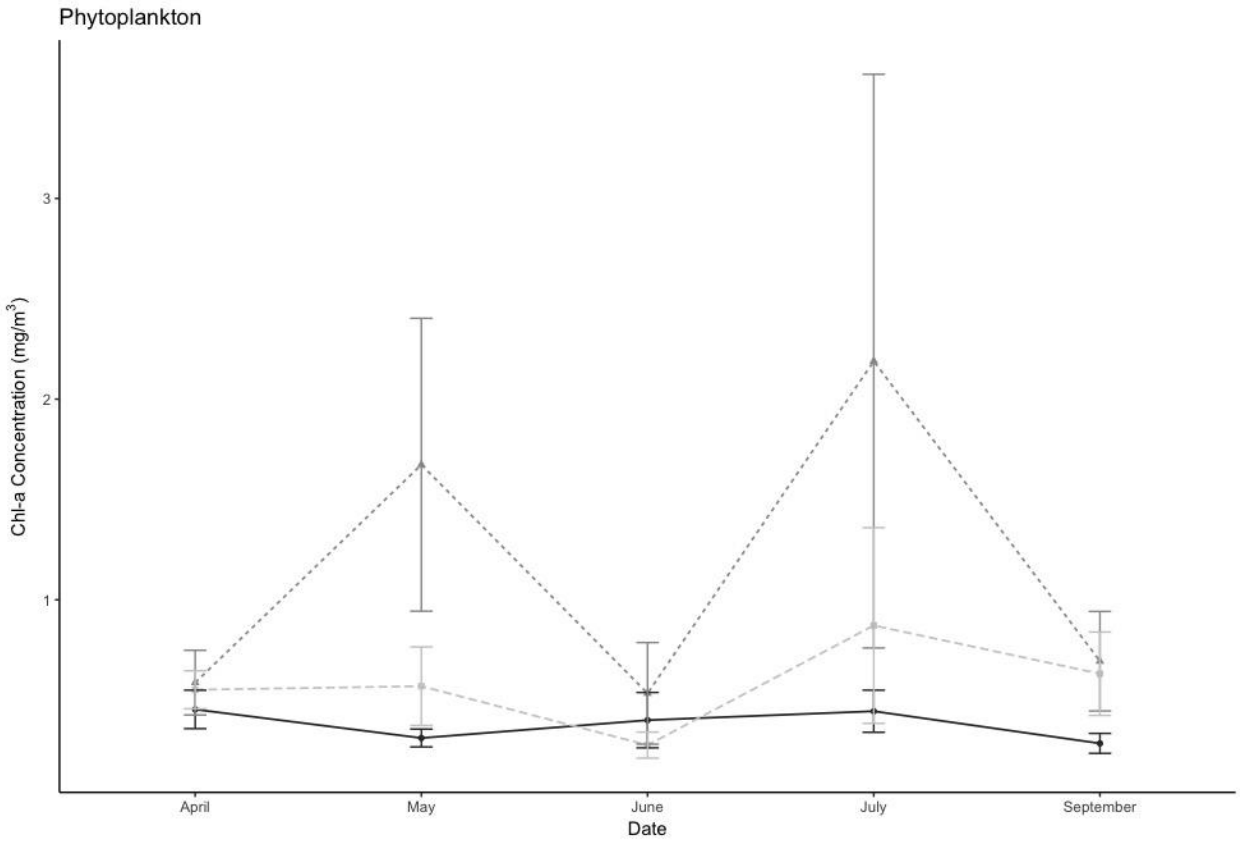

Figure 5. Mean ± SE chlorophyll-*a* concentrations from pelagic phytoplankton. Control treatments are noted by a solid black line with circles, High size variation treatments by a dark grey dotted line with triangles, and Low size variation treatments by a light grey dashed line with squares.

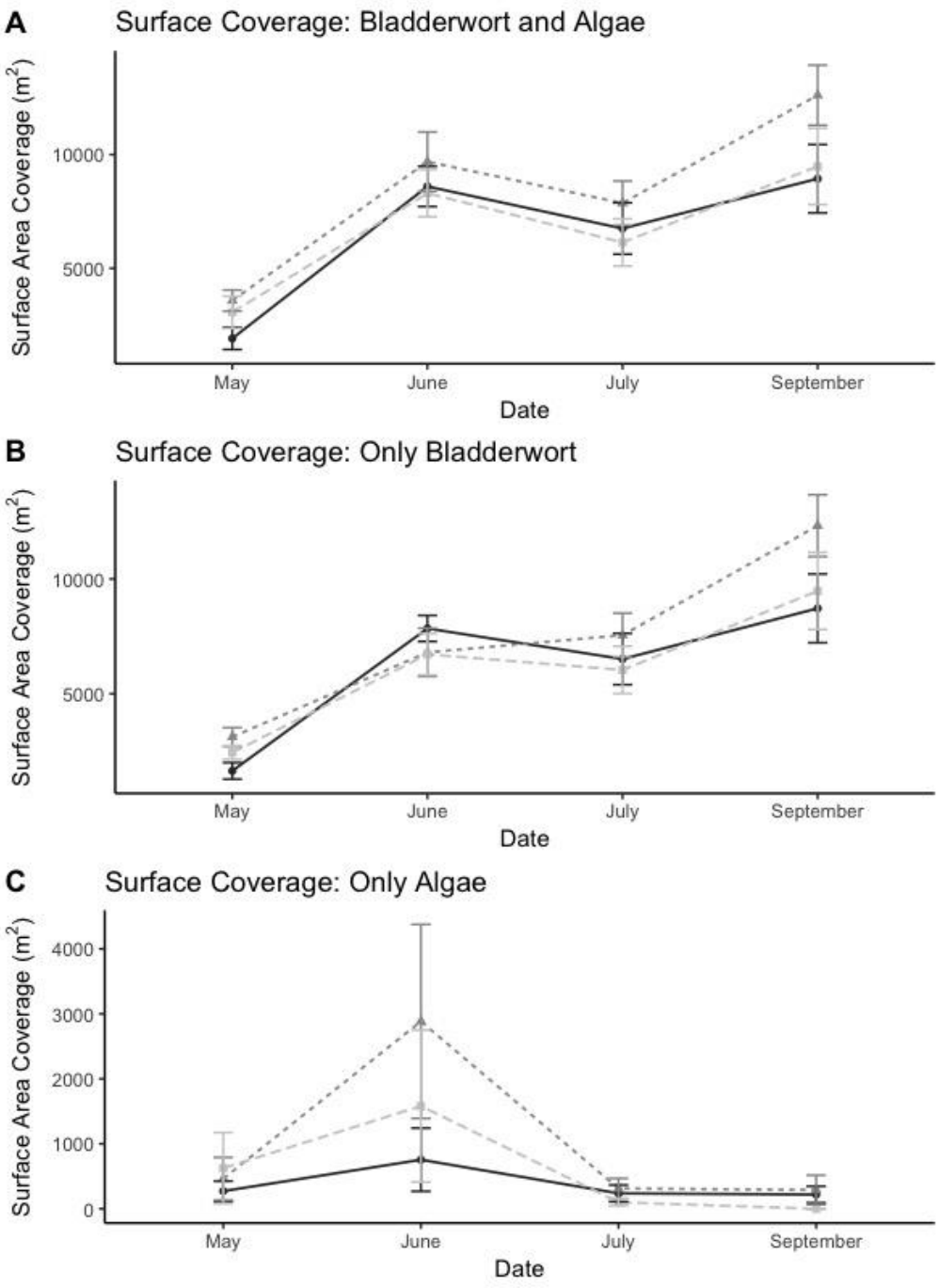

Figure 6. Mean ± SE of surface area coverage of the mesocosms by vegetation grouped by total surface area coverage (A) of combined mats of bladderwort and algae, bladderwort alone (B) and algae alone (C). Control treatments are noted by a solid black line with circles, High size variation treatments by a dark grey dotted line with triangles, and Low size variation treatments by a light grey dashed line with squares.

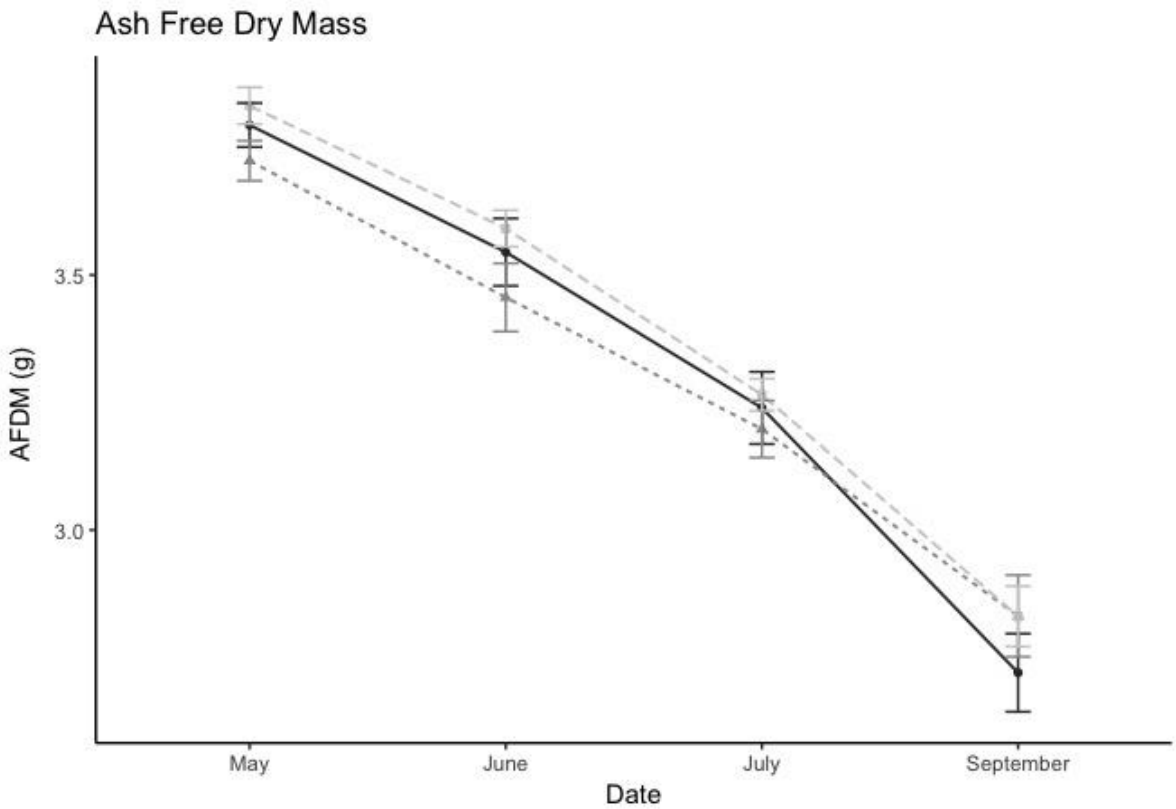

Figure 7. Mean ± SE of ash-free dry mass of leaf packs over time. Control treatments are noted by a solid black line with circles, High size variation treatments by a dark grey dotted line with triangles, and Low size variation treatments by a light grey dashed line with squares.

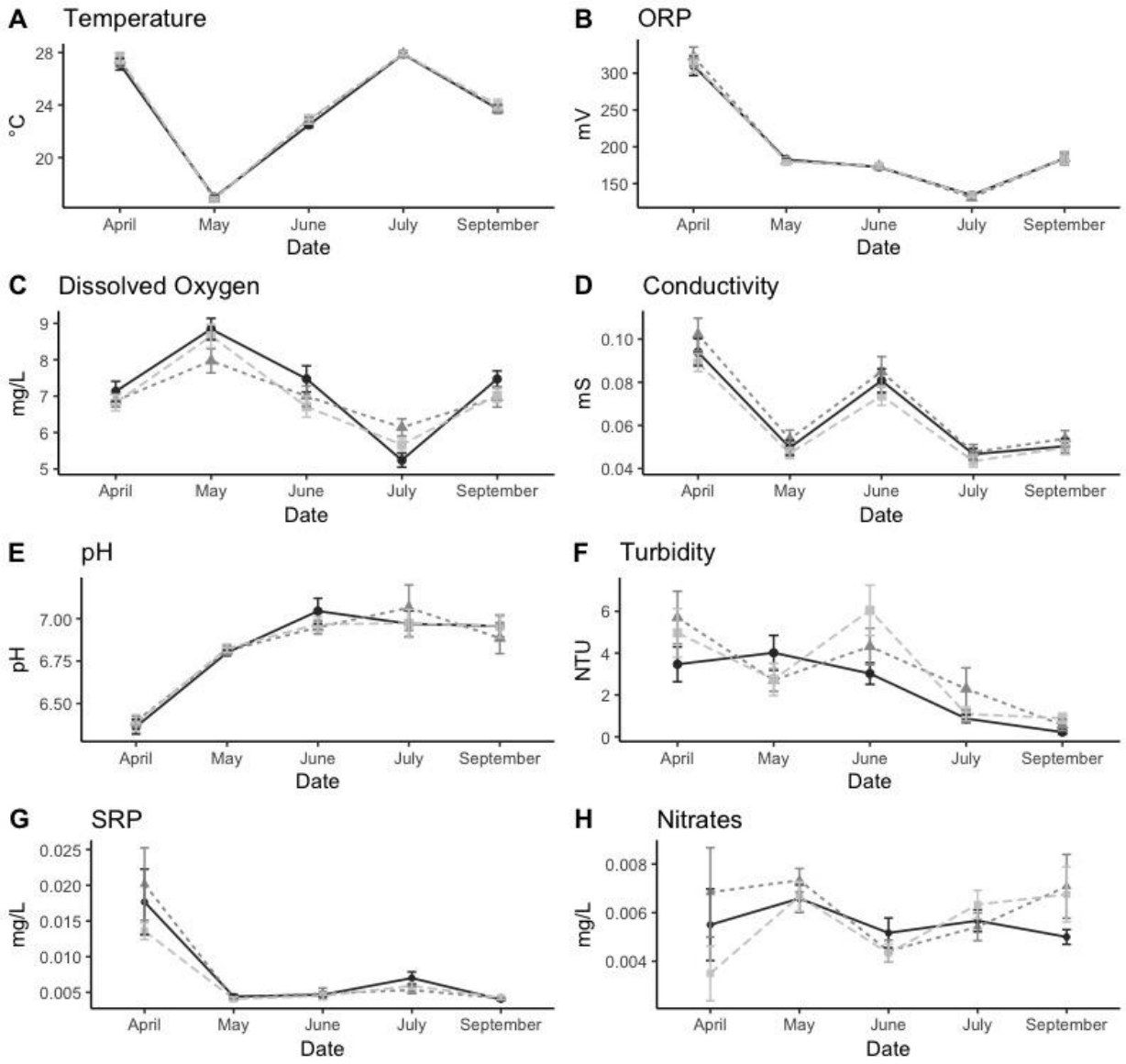

Figure 8. Mean ± SE of eight water quality parameters over the five sample dates. Shown are temperature (A), oxidation-reduction potential (B), dissolved oxygen (C), specific conductivity (D), pH (E), turbidity (F), soluble reactive phosphorous (G), and nitrate/nitrite concentrations (H). Control treatments are noted by a solid black line with circles, High size variation treatments by a dark grey dotted line with triangles, and Low size variation treatments by a light grey dashed line with squares.

LITERATURE CITED

Altig, R., M. R. Whiles, and C. L. Taylor. 2007. What do tadpoles really eat? Assessing the trophic status of an understudied and imperiled group of consumers in freshwater habitats. Freshwater Biology 52:386–395.

Anderson, T. L., and H. H. Whiteman. 2015. Non-additive effects of intra- and interspecific competition between two larval salamanders. Journal of Animal Ecology 84:765–772.

Arar, E. J., and G. B. Collins. 1997. Method 445.0: Chlorophyll A. US EPA.

Bardwell, J. H., C. M. Ritzi, and J. A. Parkhurst. 2007. Dietary selection among different size classes of larval Ambystoma jeffersonianum (Jefferson salamanders). Northeastern Naturalist 14:293–299.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Baumgärtner, D., and K. O. Rothhaupt. 2003. Predictive Length-Dry Mass Regressions for Freshwater Invertebrates in a Pre-Alpine Lake Littoral. International Review of Hydrobiology 88:453–463.

Benfield, E. F. 2006. Decompositon of Leaf Material. Pages 711–719. Methods in Stream Ecology.

Benke, A. C., A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length-Mass Relationships for Freshwater Macroinvertebrates in North America with Particular Reference to the Southeastern United States. Journal of the North American Benthological Society 18:308–343.

Beschta, R. L., and W. J. Ripple. 2012. The role of large predators in maintaining riparian plant communities and river morphology. Geomorphology 10.1016/j.

Blaustein, L., J. Friedman, and T. Fahima. 1996. Larval Salamandra Drive Temporary Pool Community Dynamics: Evidence from an Artificial Pool Experiment. Oikos 76:392–402.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution 24:127–135.

Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. W. Rudolf, S. J. Schreiber, M. C. Urban, and D. A. Vasseur. 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology & Evolution 26:183–192.

Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. L. Forister. 2003. The Ecology of Individuals: Incidence and Implications of Individual Specialization. The American Naturalist 161:1–28.

Borer, E. T., E. W. Seabloom, J. B. Shurin, K. E. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2005. What determines the strength of a trophic cascade? Ecological Society of America 86:528–537.

Bronmark, C., S. D. Rundle, and A. Erlandsson. 1991. Interactions between Freshwater Snails and Tadpoles: Competition and Facilitation. Oecologia 87:8–18.

Brunkow, P. E., and J. P. Collins. 1996. Effects of Individual Variation in Size on Growth and Development of Larval Salamanders. Ecology 77:1483–1492.

Carlson, B. E., and T. Langkilde. 2017. Body size variation in aquatic consumers causes pervasive community effects, independent of mean body size. Ecology and Evolution:1–13.

Carpenter, S. R., J. J. Cole, J. R. Hodgson, J. F. Kitchell, M. L. Pace, D. Bade, K. L. Cottingham, T. E. Essington, J. N. Houser, and D. E. Schindler. 2001. Trophic Cascades, Nutrients, and Lake Productivity: Whole-Lake Experiments. Ecological Monographs 71:163–186.

Casini, M., J. Lövgren, J. Hjelm, M. Cardinale, J.-C. Molinero, and G. Kornilovs. 2008. Multi-level trophic cascades in a heavily exploited open marine ecosystem. Proceedings of the Royal Society B 275:1793–1801.

Collins, J. P., and J. R. Holomuzki. 1984. Intraspecific variation in diet within and between trophic morphs in larval tiger salamanders (Ambystoma tigrinium nebulosum). Canadian Journal of Zoology 62:168–174.

Davenport, J. M., and D. R. Chalcraft. 2013. Nonconsumptive effects in a multiple predator system reduce the foraging efficiency of a keystone predator. Ecology and Evolution 3:3063–3072.

Davenport, J. M., and A. W. Riley. 2017. Complex inter-Kingdom interactions: carnivorous plants affect growth of an aquatic vertebrate. Journal of Animal Ecology 86:484–489.

DeLong, J. P., B. Gilbert, J. B. Shurin, V. M. Savage, B. T. Barton, C. F. Clements, A. I. Dell, H. S. Greig, C. D. G. Harley, P. Kratina, K. S. McCann, T. D. Tunney, D. a. Vasseur, and M. I. O'Connor. 2015. The Body Size Dependence of Trophic Cascades. The American Naturalist 185:354–366.

Dodson, S. I. 1974. Zooplankton Competition and Predation: An Experimental Test of the Size-Efficiency. Ecology 55:605–613.

Doyle, J. M., J. R. Nolan, and H. H. Whiteman. 2010. Effects of Relative Size on Growth Rate and Time to Metamorphosis in Mole Salamanders (Ambystoma talpoideum). Journal of Herpetology 44:601–609.

Doyle, J. M., and H. H. Whiteman. 2008. Paedomorphosis in Ambystoma talpoideum: Effects of initial body size variation and density. Oecologia 156:87–94.

Eaton, A. D., L. S. Clesceri, A. E. Greenberg, and M. A. H. Franson. 1998. Standard methods for the examination of water and wastewater.

Ellis, B. K., J. A. Stanford, D. Goodman, C. P. Stafford, D. L. Gustafson, D. A. Beauchamp, D. W. Chess, J. A. Craft, M. A. Deleray, and B. S. Hansen. 2011. Long-term effects of a trophic cascade in a large lake ecosystem. Proceedings of the National Academy of Sciences of the United States of America 108:1070–1075.

Estes, J. A., and D. O. Duggins. 1995. Sea otters and kelp forests in Alaska: Generality and variation in a community ecological paradigm. Ecological Monographs 65:75–100.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, and D. A. Wardle. 2011. Trophic downgrading of planet Earth. Science 333:301–306.

Frank, K. T., B. Petrie, J. S. Choi, and W. C. Leggett. 2005. Trophic cascades in a formerly cod-dominated ecosystem. Science 308:1621–1623.

Geraldi, N. R. 2015. Prey size structure diminishes cascading effects by increasing interference competition and predation among prey. Ecology 96:2533–2543.

González-Suárez, M., S. Bacher, and J. M. Jeschke. 2015. Intraspecific Trait Variation Is Correlated with Establishment Success of Alien Mammals. The American Naturalist 185:737–746.

Guiral, D., and C. Rougier. 2007. Trap size and prey selection of two coexisting bladderwort (Utricularia) species in a pristine tropical pond (French Guiana) at different trophic levels. International Journal of Limnology 43:147–159.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community Structure, Population Control, and Competition. The American Naturalist 94:421–425.

Harms, S. 2002. The effect of bladderwort (Utricularia) predation on microcrustacean prey. Freshwater Biology 47:1608–1617.

Holomuzki, J. R., and J. P. Collins. 1987. Trophic Dynamics of a Top Predator, Ambystoma-Tigrinum-Nebulosum (Caudata, Ambystomatidae), in a Lentic Community. Copeia 1987:949–957.

Holt, R. D., and G. A. Polis. 1997. A Theoretical Framework for Intraguild Predation. The American Naturalist 149:745–764.

Howeth, J. G., and M. A. Leibold. 2008. Planktonic dispersal dampens temporal trophic cascades in pond metacommunities. Ecology Letters 11:245–257.

Ingram, T., W. E. Stutz, and D. I. Bolnick. 2011. Does intraspecific size variation in a predator affect its diet diversity and top-down control of prey? PLoS ONE 6.

Iwai, N., and T. Kagaya. 2007. Positive indirect effect of tadpoles on a detritivore through nutrient regeneration. Oecologia 152:685–694.

Iwai, N., T. Kagaya, and R. A. Alford. 2012. Feeding by omnivores increases food available to consumers. Oikos 121:313–320.

Johnson, E. B., P. Bierzychudek, and H. H. Whiteman. 2003. Potential of prey size and type to affect foraging asymmetries in tiger salamander (*Ambystoma tigrinum nebulosum*) larvae. Canadian Journal of Zoology 81:1726–1735.

Keiser, C. N., J. B. Slyder, W. P. Carson, and J. N. Pruitt. 2015. Individual differences in predators but not producers mediate the magnitude of a trophic cascade. Arthropod-Plant Interactions 9:225–232.

Krenek, L., and V. H. W. Rudolf. 2014. Allometric scaling of indirect effects: Body size ratios predict non-consumptive effects in multi-predator systems. Journal of Animal Ecology 83:1461–1468.

Lamberti, G. A., and V. H. Resh. 1985. Comparability of introduced tiles and natural substrates for sampling lotic bacteria, algae and macroinvertebrates. Freshwater Biology 15:21–30.

Lenth, R. V. 2016. Least-Squares Means: The *R* Package lsmeans. Journal of Statistical Software 69:1–33.

Lichstein, J. W., J. Dushoff, S. A. Levin, and S. W. Pacala. 2007. Intraspecific Variation and Species Coexistence. The American Naturalist 170:807–818.

McCallister, C. T., and S. E. Trauth. 1996. Food habits of paedomorphic mole salamanders, Ambystoma talpoideum (Caudata: Ambystomatidae), from northeastern Arkansas. The Southwestern Naturalist 41:62–64.

McCauley, E., R. M. Nisbet, W. W. Murdoch, A. M. De Roos, and W. S. C. Gurney. 1999. Large-amplitude cycles of Daphnia and its algal prey in enriched environments. Nature 402:653–656.

Merritt, R. W., and K. W. Cummins. 1996. An introduction to the aquatic insects of North America. Kendall Hunt.

Miller, T. E. X., and V. H. W. Rudolf. 2011. Thinking inside the box: Community-level consequences of stage-structured populations. Trends in Ecology and Evolution 26:457–466.

Mittelbach, G. G. 1981. Foraging Efficiency and Body Size: A Study of Optimal Diet and Habitat Use by Bluegills. Ecology 62:1370–1386.

Morin, P. J. 1983. Predation, Competition, and the Composition of Larval Anuran Guilds. Ecological Monographs 53:119–138.

Morin, P. J., H. M. Wilbur, and R. N. Harris. 1983. Salamander Predation and the Structure of Experimental Communities: Responses of Notophthalmus and Microcrustacea. Ecology 64:1430–1436.

Mott, C. L., and T. J. Maret. 2011. Species-Specific Patterns of Agonistic Behavior among Larvae of Three Syntopic Species of Ambystomatid Salamanders. Copeia 2011:9–17.

Nyman, S., R. F. Wilkinson, and J. E. Hutcherson. 1993. Cannibalism and Size Relations in a Cohort of Larval Ringed Salamanders (Ambystoma annulatum). Journal of Herpetology 27:78–84.

Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology & Evolution 14:483–488.

Peckarsky, B. L., C. A. Cowan, M. A. Penton, and C. Anderson. 1993. Sublethal Consequences of Stream-Dwelling Predatory Stoneflies on Mayfly Growth and Fecundity. Ecology 74:1836–1846.

Persson, L., A. M. De Roos, D. Claessen, P. Bystrom, J. Lövgren, S. Sjogren, R. Svanbäck, E. Wahlstrom, and E. Westman. 2003. Gigantic cannibals driving a whole-lake trophic cascade. Proceedings of the National Academy of Sciences of the United States of America 100:4035–4039.

Polis, G. A. 1994. Food webs, trophic cascades and community structure. Australian Journal of Ecology 19:121–136.

Polis, G. A. 1999. Why are parts of the world green? Multiple factors control productivity and distribution of biomass. Oikos 86:3–15.

Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Laliberte, and J. S. Brashares. 2009. The Rise of the Mesopredator. BioScience 59:779–791.

Regester, K. J., K. R. Lips, and M. R. Whiles. 2006. Energy flow and subsidies associated with the complex life cycle of ambystomatid salamanders in ponds and adjacent forest in southern Illinois. Oecologia 147:303–314.

Reice, S. R. 1991. Effects of Detritus Loading and Fish Predation on Leafpack Breakdown and Benthic Macroinvertebrates in a Woodland. Journal of the North American Benthological Society 10:42–56.

Resetarits, W. J., and H. M. Wilbur. 1989. Choice of Oviposition Site by Hyla Chrysoscelis: Role of Predators and Competitors. Ecology 70:220–228.

Ripple, W. J., and R. L. Beschta. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. Forest Ecology and Management 184:299–313.

Ripple, W. J., J. A. Estes, O. J. Schmitz, V. Constant, M. J. Kaylor, A. Lenz, J. L. Motley, K. E. Self, D. S. Taylor, and C. Wolf. 2016. What is a Trophic Cascade? Trends in Ecology & Evolution 31:842–849.

De Roos, A. M., L. Persson, and E. McCauley. 2003. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. Ecology Letters 6:473–487.

Rowland, F. E., M. B. Rawlings, and R. D. Semlitsch. 2017. Joint effects of resources and amphibians on pond ecosystems. Oecologia 183:237–247.

Ruel, J. J., and M. P. Ayres. 1999. Jensen ' s inequality predicts effects of environmental variation. Trends in Ecology and Evolution 5347:361–366.

Rudolf, V. H. W. 2007. Consequences of stage-structured predators: Cannibalism, behavioral effects, and trophic cascades. Ecology 88:2991–3003.

Rudolf, V. H. W., and K. D. Lafferty. 2011. Stage structure alters how complexity affects stability of ecological networks. Ecology Letters.

Rudolf, V. H. W., and N. L. Rasmussen. 2013a. Ontogenetic functional diversity: Size structure of a keystone predator drives functioning of a complex ecosystem. Ecology 94:1046–1056.

Rudolf, V. H. W., and N. L. Rasmussen. 2013b. Population structure determines functional differences among species and ecosystem processes. Nature Communications 4:1–7.

Ruetz, C. R., R. M. Newman, and B. Vondracek. 2002. Top-down control in a detritus-based food web: Fish, shredders, and leaf breakdown. Oecologia 132:307–315.

Sabo, J. L., J. L. Bastow, and M. E. Power. 2002. Length – mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. Journal of the North American Benthological Society 21:336–343.

Schiesari, L., E. E. Werner, and G. W. Kling. 2009. Carnivory and resource-based niche differentiation in anuran larvae: Implications for food web and experimental ecology. Freshwater Biology 54:572–586.

Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ : 25 years of image analysis. Nature Methods 9:671–675.

Seale, D. B. 1980. Influence of Amphibian Larvae on Primary Production, Nutrient Flux, and Competition in a Pond Ecosystem. Ecology 61:1531–1550.

Semlitsch, R. D. 1985. Reproductive strategy of a facultatively paedomorphic salamander Ambystoma talpoideum. Oecologia 65:305–313.

Shaffer, H. B., R. A. Alford, B. D. Woodward, S. J. Richards, R. G. Altig, and C. Gascon. 1994. Quantitative sampling of amphibian larvae. *In* W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster (eds.), Measuring and Monitoring Biological Diversity Standard Methods for Amphibians: 130–141.

Shaffery, H. M., and R. A. Relyea. 2016. Dissecting the smell of fear from conspecific and heterospecific prey: investigating the processes that induce anti-predator defenses. Oecologia 180:55–65.

Shurin, J. B., and E. T. Borer. 2002. A cross ecosystem comparison of the strength of trophic cascades. Ecology Letters 5:785–791.

Siefert, A., and M. E. Ritchie. 2016. Intraspecific trait variation drives functional responses of old-field plant communities to nutrient enrichment. Oecologia 181:245–255.

Sih, A., P. Crowley, M. McPeek, J. Petranka, and K. Strohmeier. 1985. Predation, Competition, and Prey Communities: A Review of Field Experiments. Annual Review of Ecology and Systematics 16:269–311.

Simonis, J. L. 2013. Predator ontogeny determines trophic cascade strength in freshwater rock pools. Ecosphere 4:1–25.

Sitvarin, M. I., A. L. Rypstra, and J. D. Harwood. 2016. Linking the green and brown worlds through nonconsumptive predator effects. Oikos 125:1057–1068.

Soule, M. E., D. T. Bolger, A. C. Alberts, J. Wright, and S. Hill. 1988. Reconstructed Dynamics of Rapid Extinctions of Chaparral-Requiring Birds in Urban Habitat Islands. Conservation Biology 2:75–92.

Stibor, H., O. Vadstein, S. Diehl, A. Gelzleichter, T. Hansen, F. Hantzsche, A. Katechakis, B. Lippert, K. Løseth, C. Peters, W. Roederer, M. Sandow, L. Sundt-Hansen, and Y. Olsen. 2004. Copepods act as a switch between alternative trophic cascades in marine pelagic food webs. Ecology Letters 7:321–328.

Stoffels, R. J., S. Karbe, and R. A. Paterson. 2003. Length-mass models for some common New Zealand littoral-benthic macroinvertebrates, with a note on within-taxon variability in parameter values among published models. New Zealand Journal of Marine and Freshwater Research 37:449–460.

Strong, D. R. 1992. Are Trophic Cascades All Wet? Differentiation and Donor- Control in Speciose Ecosystem. Ecology 73:747–754.

Svanbäck, R., and L. Persson. 2004. Individual diet specialization, niche width and population dynamics: Implications for trophic polymorphisms. Journal of Animal Ecology 73:973–982.

Taylor, B. E., R. A. Estes, J. Pechmann, and R. D. Semlitsch. 1988. Trophic relations in a temporary pond: larval salamanders and their microinvertebrate prey. Canadian Journal of Zoology 66:2191–2198.

Terborgh, J., L. Lopez, P. Nuñez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. Science (New York, N.Y.) 294:1923–1926.

Venables, W. N., and B. D. Ripley. 2002. Modern Applied Statistics with S. Fourth. Springer, New York.

Vinyard, G. 1979. An Ostracod (Cypriodopsis vidua) Can Reduce Predation from Fish by Resisting Digestion. The American Midland Naturalist 102:188–190.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology Evolution and Systematics 15:393–425.

Wetzel, R. G., and G. E. Likens. 1991. Collection, Enumeration, and Biomass of Zooplankton. Page Limnological Analyses.

Whiteman, H. H. 1994. Evolution of Facultative Paedomorphosis in Salamanders. The Quarterly Review of Biology 69:205–221.

Whiteman, H. H., S. A. Wissinger, and W. S. Brown. 1996. Growth and foraging consequences of facultative paedomorphosis in the tiger salamander, Ambystoma tigrinum nebulosum. Evolutionary Ecology 10:433–446.

Whiteman, H. H., J. P. Sheen, E. B. Johnson, A. VanDeusen, R. Cargille, and T. Sacco. 2003. Heterospecific Prey and Trophic Polyphenism in Larval Tiger Salamanders. Copeia 2003:56–67.

Wickham, H. 2009. Elegant Graphics for Data Analysis. Springer-Verlag New York.

Wilson, D. S. 1975. The Adequacy of Body Size as a Niche Difference. The American Naturalist 109:769–784.

Wissinger, S. A., A. J. Bohonak, H. H. Whiteman, and W. S. Brown. 1999. Subalpine Wetlands in Colorado: Habitat Permanence, Salamander Predation, and Invertebrate Communities. Invertebrates in Freshwater Wetlands of North America. 757–790.

Wissinger, S. A., H. H. Whiteman, M. Denoël, M. L. Mumford, and C. B. Aubee. 2010. Consumptive and nonconsumptive effects of cannibalism in fluctuating age-structured populations. Ecological Society of America 91:549–559.

Wolkovich, E. M., S. Allesina, K. L. Cottingham, J. C. Moore, S. A. Sandin, and C. de Mazancourt. 2014. Linking the green and brown worlds: the prevalence and effect of multichannel feeding in food webs. Ecology 95:3376–3386.

Woodward, G., B. Ebenman, M. Emmerson, J. M. Montoya, J. M. Olesen, A. Valido, and P. H. Warren. 2005. Body size in ecological networks. Trends in Ecology and Evolution 20.

Woodward, G., and A. G. Hildrew. 2002. Body-size determinants of niche overlap and intraguild predation within a complex food web. Journal of Animal Ecology 71:1063–1074.