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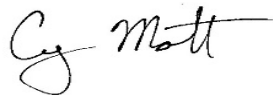
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BODY SIZE AND HABITAT SHADING INFLUENCE THE CONSUMPTIVE AND
NON-CONSUMPTIVE EFFECTS OF WOOD FROG (*LITHOBATES SYLVATICUS*)
TADPOLES ON AQUATIC INVERTEBRATE COMMUNITIES

BY

BRADY P. PARLATO

THESIS APPROVED:



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BRADY P. PARLATO

Submitted to the Faculty of the Graduate School of
Eastern Kentucky University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

May 2022

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DEDICATION

I dedicate this document to my mother, Jacque Compton, and my father, Jason Parlato, for always supporting my interest in the natural world. Thank you for your never-ending patience and guidance throughout my journey. I did my best to leave no stone unturned.

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ABSTRACT

Consumptive (direct) effects of predation have been well-studied in most aquatic systems, but non-consumptive (indirect) effects on prey have only recently received limited attention in some groups. As aquatic consumers, tadpoles have traditionally been considered strict herbivores, leaving their predatory impacts via consumptive and non-consumptive interactions on aquatic invertebrates largely unexplored. The objectives of this study were to quantify omnivory among wood frog (*Lithobates sylvaticus*) tadpoles, determine their consumptive and non-consumptive effects on invertebrate communities, and investigate whether such effects are mediated by habitat shading and tadpole body size. *Lithobates sylvaticus* tadpoles and egg masses were randomly sampled from 11 ponds in the Daniel Boone National Forest, eastern Kentucky, USA. Tadpoles were dissected to quantify the frequency of omnivory, while egg masses were reared to hatching to create size structure. Hatched tadpoles were then employed in a fully factorial mesocosm design that manipulated tadpole presence (absent, caged, or free-swimming), body size (large or small), and canopy cover (shaded or unshaded) to determine effects on invertebrate communities. Over 70% of tadpoles in natural ponds engaged in omnivory, primarily on zooplankton. Tadpoles in mesocosms exhibited consumptive and non-consumptive effects on invertebrate communities, with generally reduced invertebrate abundance under shaded conditions and in the presence of larger tadpoles. Larger tadpoles in unshaded conditions also exhibited higher survival and maintained larger sizes, but smaller tadpoles in unshaded conditions grew more quickly. This study stresses the ecological importance of tadpoles, given their roles as predators of, and competitors with, aquatic invertebrates.

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I. Introduction

Predation is an important ecological factor in maintaining the structure and function of aquatic systems because of its pervasive effects on prey communities (Shurin 2001, Shurin *et al.* 2002, Preisser *et al.* 2009, Pessarrodona *et al.* 2019). Studies of predation in aquatic ecosystems have largely focused on its consumptive (i.e., direct) effects, which include limiting prey recruitment (Juanes and Conover 1995) and initiating top-down trophic cascades that can alter the relative abundance, species richness, and ecological functioning of lower trophic levels (Martin *et al.* 1992, Hecnar and M'Closkey 1997, Connell 1998). More recent studies of predation in aquatic systems have highlighted the prevalence and importance of non-consumptive (i.e., indirect, or trait-mediated) predator effects that occur outside of the consumption of prey. Predator presence and associated cues regarding predation risk cause prey to change patterns of foraging and habitat selection to avoid detection (Magoulick 2004, Strobbe *et al.* 2011). Such changes in behavior can limit food intake (Peacor and Werner 2000) and force prey into alternative habitats (Jordan *et al.* 1997), reducing growth rates of surviving prey under high predator densities (Heins *et al.* 2016) and subsequently altering species diversity, or the range of species found in a particular place, in aquatic ecosystems (Thorpe and Cothran 1984). Detection of cues associated with predation risk can lead to the expression of costly inducible defense mechanisms, such as defensive spines / spikes (Laforsch and Tollrian 2004, Petrušek *et al.* 2009), disruptive color patterns (Toledo and Haddad 2009), and altered body shapes, sizes, and growth rates (McCollum and Van

Buskirk 1996, McCollum and Leimberger 1997, Benard 2004), which can have reciprocal consequences for predator communities.

Consumptive and non-consumptive effects of predators have been relatively well-studied in many terrestrial systems (Prevosti *et al.* 2013, Hite *et al.* 2018, Say-Sallaz *et al.* 2019), but similar research in aquatic systems is mainly limited to fish (Wagner *et al.* 2004, Kindinger and Albins 2017), salamanders (Whiteman *et al.* 2003, Wissinger *et al.* 2010), and odonate nymphs (Peacor and Werner 2000). Studies on consumptive and non-consumptive predatory effects of anuran larvae (i.e., tadpoles) are generally lacking, likely due to their historic label as strict herbivores (Kupferberg 1997, Altig *et al.* 2007). Despite the lack of evidence for predatory effects of tadpoles in classic literature, recent research has demonstrated that tadpoles are frequently opportunistic omnivores, consuming algae, as well as zooplankton, macroinvertebrates, and other amphibian larvae (Whiles *et al.* 2010, Schalk *et al.* 2017, Montaña *et al.* 2019). Tadpoles of some anuran species are primarily carnivorous (Schiesari *et al.* 2009, Levis *et al.* 2015), with select taxa exhibiting cannibalism (e.g., Petranka and Thomas 1995, Pfennig 1999, Jefferson *et al.* 2014). Predatory tadpoles likely also induce trait-mediated, non-consumptive effects on aquatic organisms. For example, when odonate predators restrict foraging times and microhabitats of tadpole prey, larger tadpoles outcompete smaller conspecifics for food (Peacor and Werner 2000), suggesting predatory tadpoles could induce similar trait-mediated, non-consumptive effects on invertebrate prey. Given this evidence, tadpoles may exhibit diverse consumptive and non-consumptive predatory effects on invertebrates

that occur alongside their traditionally assumed competitive effects (Figure 1¹; Brönmark *et al.* 1991, Holomuzki and Hemphill 1996, Mokany and Shine 2003a).

Consumptive and non-consumptive effects of tadpoles would act in concert with established competitive relationships between tadpoles and freshwater invertebrates, but it is unknown if the non-consumptive effects of tadpoles alter prey population dynamics additively with or independently of competitive effects (Sheriff *et al.* 2020). Competition between tadpoles and invertebrates for planktonic algae, periphyton, and biofilms in freshwater systems is well-documented. Tadpoles limit biofilm availability for macroinvertebrates, displace them from feeding areas (Atwood and Richardson 2012), and reduce rates of macroinvertebrate egg production through competition for periphyton (Brönmark *et al.* 1991, Holomuzki and Hemphill 1996). Cases of extreme competition between tadpoles and freshwater invertebrates can lead to intraguild predation, or predation among species within the same trophic level. For example, tadpoles compete with mosquito larvae for algae in phytotelmata, but will consume mosquitoes if resources are limited (von May *et al.* 2009). Overall, jointly characterizing the competitive, as well as consumptive and non-consumptive predatory effects, of tadpoles on freshwater invertebrates will facilitate a more complete understanding of their diverse trophic roles.

Although little is known regarding the consumptive and non-consumptive predatory effects of tadpoles on freshwater invertebrate communities, limited investigations of such trophic interactions suggest they are largely context-dependent. Tadpole trophic interactions are mediated by age and body size, as younger (i.e., smaller) tadpoles often cannot prey on, and instead serve as prey for, macroinvertebrates

¹ All Tables and Figures are included in the Appendices

(Blaustein and Margalit 1996), but later develop into predators that feed on macroinvertebrates (Jara 2008). Although such ontogenetic dietary shifts and their ecological consequences are well-known among larval salamanders (Leff and Bachmann 1986, Denoël *et al.* 2006, Schriever and Williams 2013), there is less evidence of similar phenomena among many tadpole species. In addition to tadpole body size, habitat shading can also affect tadpole trophic dynamics, as tadpoles occupy higher trophic levels under higher levels of canopy coverage (Schalk *et al.* 2017), because lower levels of primary productivity under shade increase the need for carnivory. Complex trade-offs between herbivory and carnivory also exist, as Carreira *et al.* (2016) observed tadpoles shifting towards carnivory grew slower but were larger at metamorphosis, although others have observed opposite trends (Ramamonjisoa *et al.* 2016).

A more comprehensive understanding of the consumptive and non-consumptive predatory effects of tadpoles, and how such phenomena interact with the competitive effects of tadpoles, is important in both applied and theoretical contexts. Nearly 40% of all amphibians are in danger of extinction (Stuart *et al.* 2004, Bishop *et al.* 2012), and larval amphibians play valuable ecological roles in disease vector control (Bowatte *et al.* 2013), nutrient cycling (Montaña *et al.* 2019), and energy transfer (Regester *et al.* 2006). Investigations of the consumptive and non-consumptive predatory effects of tadpoles on invertebrate communities are needed to better understand the potential consequences of anticipated declines in amphibian population densities and / or losses in amphibian species diversity. In addition, tadpoles are often the dominant vertebrate consumers in fishless ponds (Holomuzki 1998, Mallory and Richardson 2005, Walston and Mullin 2007), and thus greater knowledge of their consumptive and non-consumptive predatory

effects would shed light on trophic dynamics in these habitats. Lastly, our limited understanding of the impacts of tadpole predation on invertebrates comes primarily from tropical, permanent aquatic systems (Ranvestel *et al.* 2004, Dutra and Callisto 2005, Altig *et al.* 2007, Whiles *et al.* 2010, Montaña *et al.* 2019), which do not reflect temperate, ephemeral habitats in important ways. Rates of leaf litterfall and levels of plant-derived detritus are greater in tropical systems (Vitousek 1984, Vitousek and Sanford 1986, Boulton *et al.* 2008), whereas freshwater invertebrates are more abundant in temperate waters (Boulton *et al.* 2008). Ephemeral habitats, where tadpoles are frequently abundant, are smaller and have fewer resources than permanent habitats, which drives more intense competition and predation among their inhabitants (Aspbury and Juliano 1998, Blaustein *et al.* 2001). Species inhabiting permanent freshwaters also differ from ephemeral freshwater species because they do not need to transition to terrestrial habitats or experience dietary shifts (Wickramasinghe *et al.* 2007, Regester *et al.* 2008).

To better understand the trophic roles of larval anurans, this study aimed to use experimental mesocosms to quantify: (1) omnivory in naturally occurring wood frog (*Lithobates sylvaticus*) tadpole populations; (2) the response of temperate, freshwater invertebrate communities to the consumptive and non-consumptive effects of wood frog tadpoles; including how these effects are mediated by shading and predator body size.

My first objective was to conduct gut content analyses on wood frog tadpoles in natural ponds to better understand their roles as predators of freshwater invertebrates. Specifically, I sought to determine the frequency of tadpole omnivory, the abundance of consumed invertebrates by taxon, whether abundances varied across ponds based on heterogeneity in pond area, and if the likelihood of omnivory in tadpoles is influenced by

tadpole morphology. I hypothesized that omnivory would be the most common dietary strategy, that relative abundances of consumed invertebrates would differ by pond surface area (i.e., greater area generally facilitates consumption of more individuals and species), and that larger tadpoles would more frequently engage in omnivory (Jara 2008). Furthermore, to determine whether mesocosms used in subsequent experiments accurately reflected natural ponds, I sought to determine whether abundances of invertebrates consumed by tadpoles differed between these venues.

Second, I used mesocosm experimental approaches to investigate the consumptive and non-consumptive predatory effects of tadpoles on freshwater invertebrate abundance and community composition, while determining how these predatory effects are influenced by habitat shading and tadpole size. I hypothesized that invertebrate abundance would be lowest at the end of the experiment in mesocosms with free-swimming tadpoles (i.e., those that could exert both consumptive and non-consumptive effects), and that invertebrate community composition would be influenced by tadpole presence. I also predicted that large tadpoles (decreased gape limitations) and shaded conditions (reduced primary productivity) would lead to the largest decreases in invertebrate abundance and alter community composition by decreasing the relative abundances of smaller, herbivorous invertebrates (i.e., these invertebrates are more easily consumed and have less available food due to low primary productivity). Environmental variables, such as temperature, were also recorded to determine any possible influence of such factors on the predator-prey interactions between tadpoles and invertebrates. Lastly, tadpole survival and growth were recorded to quantify any reciprocal effects of exposure to invertebrate prey on tadpole predators.

II. Materials and Methods

Focal Species Life History

Lithobates sylvaticus is the most widespread anuran species in North America (Martof and Humphries 1959) and tadpoles often reach higher densities in temporary ponds than top invertebrate predators (Petranka *et al.* 1994). Normally the first anuran to breed in late winter (Berven 1982) or early spring (Redmer and Trauth 2005), female *L. sylvaticus* typically produce between 700-1250 eggs per reproductive effort (Corn and Livo 1989). Eggs hatch within four weeks, and tadpoles metamorphose between 65-130 days later (Redmer and Trauth 2005). The maximum range for *L. sylvaticus* tadpole body length is 50-66 mm (Redmer 2002). Tadpoles consume mixtures of green and blue-green algae (Perez *et al.* 2013), copepods and cladocerans (Sours and Petranka 2007), midge larvae and oligochaetes (Petranka and Kennedy 1999), and even smaller conspecific (Jefferson *et al.* 2014) and heterospecific tadpoles (Sours and Petranka 2007). Tadpoles are active, diurnal foragers, but will decrease activity and resource consumption in the presence of predators (Relyea 2002), such as ambystomatid salamander larvae (Walls and Williams 2001) and odonate nymphs (Eaton and Paszkowski 1999). Although tadpoles can reach average densities of ~200-1,800 individuals / m² (Biesterfeldt *et al.* 1993, Hall *et al.* 2018), maximum densities of ~8,900 individuals / m² have been reported (Biesterfeldt *et al.* 1993). Regarding factors related to population sizes, tadpole densities are negatively correlated with size at metamorphosis and survival (Berven 1982). On average, 65.7% of hatchling *L. sylvaticus* survive to metamorphosis (Seigel 1983).

Objective 1: Gut Content Analyses of *Lithobates sylvaticus* Tadpoles

From each of ten ephemeral ponds in the Daniel Boone National Forest (DBNF), Cumberland Ranger District, eastern Kentucky, USA, 20 *L. sylvaticus* tadpoles were collected on April 8th and 10th, 2021. Only ten tadpoles were collected from an 11th pond due to low densities ($N = 210$ total). Pond surface area was visually estimated, and three area classes were established: 1. Small ($\leq 10 \text{ m}^2$); 2. Intermediate ($10 \text{ m}^2 < X < 100 \text{ m}^2$); 3. Large ($\geq 100 \text{ m}^2$). Tadpoles were collected using 1-mm mesh dip nets, immediately anesthetized and euthanized with a 250-mg L^{-1} aqueous solution of benzocaine, and preserved in 10% buffered formalin (Steiner 2007). Each tadpole was photographed and measured (mm head width, tailfin height, total body length, and gut length of tadpoles) using ImageJ to investigate any possible correlation between tadpole morphology and diet (Rueden *et al.* 2017). For example, tadpoles exhibiting tendencies towards herbivory over carnivory exhibit longer guts (Altig and Kelly 1974), given that amphibians cannot easily process cellulose in algae and plants. The first 10 mm of the gut were excised from each tadpole (Ocock *et al.* 2019); only materials in this part of the gut were examined because materials in the rest of the gut are typically indistinguishable (Ghioca-Robrecht and Smith 2011). Presence of invertebrates as an indication of omnivory, and invertebrate abundances by lowest useful taxon, in tadpole guts were determined under 35x dissection microscopy (Merritt and Cummins 1996, Dillard 1999, Smith 2001) per individual.

Objective 2: Consumptive and Non-consumptive Effects of Tadpole Predators

Sediments containing macroinvertebrates were collected from a forested pond in Miller Welch - Central Kentucky Wildlife Management Area (CKWMA), Waco,

Kentucky, USA on February 25th, 2021 and from eight ephemeral ponds in DBNF on March 5th and March 11th, 2021 using 1-mm mesh dip nets. Zooplankton were collected from a pond in Taylor Fork Ecological Area (TFEA), Eastern Kentucky University (EKU), Richmond, KY, USA on February 15th, 2021, from CKWMA on February 25th, 2021, and from DBNF on March 5th and 11th, 2021 using an 80- μ m Conical Fieldmaster® Student Zooplankton Net. Collected macroinvertebrates and zooplankton were kept in separate 1136-liter Rubbermaid™ holding tanks until needed, which were left uncovered to allow for colonization by additional invertebrates. On March 5th, 2021, 100 *L. sylvaticus* eggs were collected from each of ten ephemeral ponds in DBNF ($N = 1000$). Once eggs hatched, tadpoles were fed with six Purina® dog chow pellets every two days.

Between late January and mid-March 2021, 100 76-liter stock tanks (MacCourt Products, Denver, Colorado, USA) were established as mesocosms in TFEA. To stock each mesocosm, 1900 cm³ of dry leaf litter were added to all tanks on February 6th, 2021. American sycamore (*Platanus occidentalis*) and pin oak (*Quercus palustris*) leaf litter was collected from the EKU campus grounds and TFEA. Each mesocosm contained one 10 x 6 x 6-cm unglazed ceramic tile attached to the tank interior ~ 15 cm above the leaf litter at a standardized compass direction for algal colonization. After the addition of dry leaf litter, one “grab” (1215 cm³) of a Fieldmaster® Mighty Grab from the 1136-L holding tank with wet leaf litter, sediment, and macroinvertebrates, along with 250 ml of concentrated zooplankton solution from holding tanks, were added to each mesocosm on March 19th, 2021. Mesocosms were allowed three weeks to establish “normal” ecological processes before introducing tadpoles.

Ten tadpoles per mesocosm were randomly assigned to one of two experimental treatments, and a separate control group was established with no tadpoles on April 9th, 2021 (Figure 2). The two experimental treatments included a “consumptive + non-consumptive” (hereafter “C+NC”) treatment group and a solely “non-consumptive” (hereafter “NC”) treatment group. In C+NC mesocosms, tadpoles were free-swimming and able to feed on macroinvertebrates, zooplankton, plant and biofilm material, and detritus, exerting both consumptive and non-consumptive predatory effects, in addition to competitive effects, on herbivorous invertebrates. In the NC group, tadpoles were added to 25 x 25 x 25-cm basket-like cages constructed from 1.27-cm PVC pipes and 60- μ mesh netting to exclude macroinvertebrates and zooplankton (*sensu* Skelly and Werner 1990, Maher *et al.* 2013, Gallagher *et al.* 2019). Cages were added to all treatment and control mesocosms on March 25th, 2021 to account for any generalized “cage effects” on response variables. Each cage was open at the top and securely fastened over the rim of each mesocosm (Figure 2). This design: a) enabled tadpoles to surface as needed without escaping; b) allowed for the transfer of aquatic cues of predators and predation risk from the cages to macroinvertebrates and zooplankton outside of cages; and c) permitted tadpoles to feed on algae and biofilms on tank sides. Each cage was rotated 45° in the mesocosm every five days to allow tadpoles to graze new sources of algae and biofilms. Although predatory effects of tadpoles could not be isolated from competitive effects on invertebrate communities using this design, tadpoles competed for food with invertebrates across all treatments, and thus degree of competition was standardized to the best of our abilities. Cages in all mesocosms also received ~607.5 cm³ of wet leaf litter, sediment, and macroinvertebrates from a Fieldmaster® Mighty Grab from the

holding tank and 250 ml of concentrated zooplankton solution one week prior to the introduction of tadpoles. In the NC treatment, cages received crushed zooplankton from a 250-ml concentrated solution and 20 ml of a crushed commercial *Chironomus* (ELOS Fresco™) solution every five days as sources of food and aquatic cue of predation risk (*sensu* Skelly and Werner 1990, do Amaral *et al.* 2018, Gallagher *et al.* 2019).

To investigate whether differences in tadpole body size (which influence gape limitation and predation risk) and habitat shading (which influence light penetration, and thus primary productivity) affect their consumptive and non-consumptive predatory effects on freshwater invertebrates, two treatment levels each for tadpole size and degree of mesocosm shading were created in a 2 x 2 fully factorial design along with controls (Figure 3). In assessing the effects of tadpole body size on consumptive and non-consumptive predatory effects, two tadpole size classes, large and small, were established. To establish large and small size groups, half ($N = 500$) of the eggs initially collected were randomly added to a 1136-liter stock tank filled with rainwater and green algae at TFEA, while the other half were randomly separated into eight roughly equal groups in 42 x 29 x 15-cm plastic containers with rainwater and kept in an environmental chamber within the EKU vivarium facilities at 8°C. Eggs left outside at higher temperatures were expected to hatch / develop faster and were designated as the “large” size group, whereas those in the environmental chamber were expected to develop slower and were designated as the “small” size group. Eggs in the “small” size group were transported to another 1136-liter stock tank at TFEA on March 26th, 2021, just before hatching. All tadpoles were fed with six Purina® dog chow pellets every two days. Tadpoles were visually inspected in each tank, and only the smallest and largest tadpoles

from the “small” and “large” size groups, respectively, were included in the experiment, thus maximizing body size differences between treatments. A subset of 40 mesocosms was established, each containing ten tadpoles designated as “small”, whereas an additional 40 mesocosms each received ten tadpoles designated as “large”. To determine the influence of shading on consumptive and non-consumptive predatory effects of tadpoles on invertebrates, half ($N = 20$) of the mesocosms in each size group ($N = 40$ total) and half ($N = 10$) of the control mesocosms ($N = 20$ total) were shaded using 88% shade cloths supported by metal posts ~1.5 meters above each mesocosm. Overall, there were two control groups, one shaded and one unshaded, with ten mesocosms each, and four treatment groups, each with 20 mesocosms: 1) large tadpoles, unshaded; 2) large tadpoles, shaded; 3) small tadpoles, unshaded; and 4) small tadpoles, shaded. Each of the four treatments consisted of ten mesocosms with free-swimming tadpoles (C+NC) and ten mesocosms with caged tadpoles (NC; Figure 3).

On May 14th, 2021 (35-day study period), tadpoles were collected from tanks, anesthetized and euthanized using a 250-mg L⁻¹ aqueous solution of benzocaine, and preserved in 10% buffered formalin (Steiner 2007). Tadpoles were photographed and measured (mm) using ImageJ (Rueden *et al.* 2017) at the start and conclusion of the experiment to determine growth rates, and dissected following the same procedures outlined in Objective 1 to compare gut contents with wild-caught tadpoles. Relative fluorescence estimates (RFU) were recorded for each mesocosm using an AquaFluor® handheld fluorometer (Turner Designs, San Jose, California, USA) as an estimate of primary productivity, and temperature and % dissolved oxygen were recorded using an Oakton DO 6+ Meter (Oakton Instruments, Vernon Hills, Illinois, USA). Ceramic tiles in

each mesocosm were scraped with razorblades to collect biofilms, which were preserved in 2% glutaraldehyde, dried at 60°C for 24 hours, and weighed to determine biomass (Smith 2019). Zooplankton were collected by straining 250 ml of water in each mesocosm through an 80- μ m zooplankton net. To sample benthic macroinvertebrates, 100 ml of sediment solution were collected from each mesocosm using 1-mm mesh hand nets. Macroinvertebrates and zooplankton were euthanized and preserved in 10% buffered formalin with Rose Bengal stain, respectively, counted, identified to the lowest useful taxon level under 35x dissection microscopy using Merritt and Cummins (1996) and Smith (2001), and transferred to 70% ethanol. Abundances of collected invertebrates by taxon were compared across all tadpole cage, size, and habitat shading treatments. To estimate the “non-consumptive” effects of uncaged tadpole presence on invertebrate abundance by taxonomic group, measurements of invertebrate abundance assessed from the NC treatment were compared against those same response variable measurements from control tanks. We could not solely assess the consumptive predatory effects of tadpoles because uncaged tadpoles in the C+NC treatment will exhibit both consumptive and non-consumptive effects. Due to an inability to isolate consumptive effects, the intensity of consumptive effects alone was estimated by comparing response variable measurements between the C+NC treatment and the NC treatment (i.e., consumptive effects = (non-consumptive effects + consumptive effects of uncaged tadpoles) – (non-consumptive effects of caged tadpoles); Figure 2). In addition to the inability to isolate consumptive effects, effects of competition could not be separated from effects of tadpole predation. Because of this limitation, all estimates of consumptive and non-consumptive effects inherently contain the effects of competition between tadpoles and invertebrates.

Statistical Analyses

All statistical analyses were conducted in R version 3.6.1 with $\alpha = 0.05$ (R Core Team 2018). To determine if tadpole omnivory levels differed among natural ponds, numbers of wood frog tadpoles from each pond that had consumed invertebrate material, relative to those that did not, were counted and compared among ponds using a Chi-Square Test of Independence (function 'chisq.test'). To assess differences in tadpole foraging preferences based on heterogeneity in pond surface area, a linear mixed effects model was constructed (function 'lmer'), and subsequently summarized using an ANOVA table (function 'anova'). In this model, abundances of a) total invertebrates and b) specific invertebrate taxa consumed by individual tadpoles were compared across the pond area classes (established in Objective 1 methodology above), with blocking by 'pond identity' as a random effect to avoid pseudoreplication.

To investigate whether tadpole morphology explains variation in diet, generalized linear models with binomial error distributions were constructed between frequency of omnivory and all morphological variables described in Objective 1 (function 'glm'). An additional Chi-Square Test of Independence was conducted to determine if total abundances of invertebrates consumed by tadpoles differed between ponds and mesocosms. For all analyses, consumed invertebrate abundances were log transformed. Shapiro-Wilks tests of normality (function 'shapiro.test') and Levene's tests of homogeneity of variances (function 'leveneTest') were used to test model assumptions.

The data obtained from the mesocosm experiment were separated into two datasets to independently assess the consumptive and non-consumptive predatory effects

of tadpoles and the interactive effects with tadpole body size and habitat shading. For the first set of analyses, the dataset was restricted to unshaded controls, unshaded mesocosms with large, caged tadpoles, and unshaded mesocosms with large, free-swimming tadpoles ($N = 30$), to isolate predatory effects independent of tadpole body size and habitat shading. All models in these analyses included only the effect of cage vs. no cage as the predictor variable. For the second set of analyses, the dataset included all mesocosms ($N = 100$). In these analyses, all three treatment effects were included as predictor variables in the model (cage, shading, and tadpole body size). For both sets of analyses, the following four response variables were tested: 1) macroinvertebrate abundance, 2) zooplankton abundance, 3) environmental variables (biofilm mass, relative fluorescence, % dissolved oxygen, and temperature), and 4) tadpole survival and growth rates, with tadpole cage treatment levels (no tadpoles, caged tadpoles, free-swimming tadpoles), tadpole size treatment levels (large or small), and habitat shading treatment levels (shaded or unshaded) serving as experimental variables. To increase statistical power (Chalcraft and Resetarits Jr. 2003), since the response variables were related, separate MANOVAs (function 'manova') were performed on each subset of response variables. When MANOVA indicated significant treatment effects, subsequent one-way ANOVAs and Holm's pairwise t-tests (function 'pairwise.t.test' with Holm's correction) were conducted to identify significant differences among treatment levels (Helsel *et al.* 2020, Medina *et al.* 2021). Response variables were log (discrete variables) and Tukey's Ladder of Powers (continuous variables) transformed and subjected to Shapiro-Wilks tests of normality and Levene's tests of homogeneity of variances to meet model assumptions. Because tadpole body measurements were analyzed on an individual basis, a separate

linear mixed effects model (function “lmer”) with blocking by ‘mesocosm ID’ as a random effect, was constructed prior to running ANOVAs to avoid pseudoreplication.

To evaluate the effects of the treatments (tadpole cage, habitat shading, and tadpole body size) on the invertebrate community composition, an Analysis of Similarity (ANOSIM; function ‘anosim’) was performed. The ‘Bray-Curtis’ distance measure was selected for this analysis because it is appropriate for use with categorical predictor variables and relative abundances. A separate ANOSIM was performed for the macroinvertebrate community and the zooplankton community.

To visualize the effects of the treatments (tadpole cage treatment, habitat shading, and tadpole size) on macroinvertebrate and zooplankton community composition, separate capscale ordination plots (function ‘ord.plot’) were constructed. The distance measure selected for each capscale ordination was also ‘Bray-Curtis’ because of its common application to categorical and non-continuous ecological data, such as cage treatment and relative abundances of invertebrates among different treatments.

III. Results

Objective 1: Gut Content Analyses of *Lithobates sylvaticus* Tadpoles

Tadpoles collected from DBNF engaged in omnivory more often than other dietary strategies, and occurrence of omnivory varied based on tadpole morphology. Among 11 ponds and 210 individuals, 70.48% of tadpoles engaged in omnivory on some form of invertebrate matter (e.g., Figures 4 and 5). Invertebrates consumed by tadpoles spanned seven taxa, including Cladocera (3.97 ± 0.265), Ostracoda (2.57 ± 0.109), Copepoda (3.00 ± 0.001), Chironomidae (1.00 ± 0.001), Nematoda (4.00 ± 0.101), Oligochaeta (4.67 ± 0.039), and Rotifera (1.00 ± 0.012). Numbers of tadpoles that engaged in omnivory, relative to those engaging in other dietary strategies, significantly differed among ponds ($X^2 = 98.16$, $df = 10$, $p < 0.001$; Figure 6), ranging from 10% - 100%. Tadpoles were more likely to be omnivorous as head width ($Z = 2.65$, $p = 0.008$) and tailfin height ($Z = 3.87$, $p < 0.001$) increased, but feeding habits were not influenced by tadpole body length ($Z = -1.43$, $p = 0.152$) or gut length ($Z = -0.10$, $p = 0.922$). Although total invertebrates consumed by tadpoles did not significantly differ across pond area classes (5.01 ± 0.369 ; ANOVA $F_{2,8} = 4.42$, $p = 0.053$; Figure 6), cladocerans (ANOVA $F_{2,8} = 4.59$, $p = 0.044$; Figure 7), the most consumed invertebrate taxon, varied in abundance based on pond area. Abundances of invertebrates consumed by tadpoles also differed between ponds and mesocosms ($X^2 = 274.52$, $df = 8$, $p < 0.001$), with more invertebrates being consumed per tadpole in mesocosms (7.95 ± 0.62) than natural ponds (3.53 ± 0.37).

Objective 2: Consumptive and Non-consumptive Effects of Tadpole Predators

The relative abundance of macroinvertebrate groups differed by tadpole cage treatment (MANOVA $F_{2,27} = 2.66$, $p < 0.001$; Table 1), but total macroinvertebrate abundance was not influenced (Table 1; Figure 8). Holm's pairwise t-tests indicated oligochaete eggs were more abundant in controls (39.10 ± 4.62) compared to mesocosms with caged (19.35 ± 2.14 ; $p = 0.001$) or free-swimming (11.55 ± 1.70 ; $p < 0.001$) tadpoles, respectively, and mesocosms with caged tadpoles had more oligochaete eggs than those with free-swimming tadpoles ($p = 0.031$). Although trichopterans were generally uncommon, abundances were higher in controls (2.40 ± 0.63) compared to mesocosms with caged (0.65 ± 0.27 ; $p < 0.001$) or free-swimming (0.08 ± 0.06 ; $p < 0.001$) tadpoles, respectively, although abundances did not statistically differ between treatments with tadpoles ($p = 0.063$). Chironomids were more abundant in controls (7.75 ± 1.42) compared to mesocosms with uncaged tadpoles (5.15 ± 0.96 ; $p = 0.038$), but did not differ in abundance between control and caged (5.50 ± 0.82) tadpole mesocosms ($p = 0.282$) or between tadpole treatments ($p = 0.282$).

Macroinvertebrate relative abundance also differed between the habitat shading (MANOVA $F_{1,90} = 8.78$, $p < 0.001$) and tadpole size (MANOVA $F_{1,90} = 2.84$, $p = 0.001$) treatments, and by the interaction between shading and size (MANOVA $F_{1,90} = 4.07$, $p < 0.001$; Table 1; Figure 9). Macroinvertebrate community composition differed by cage treatment (ANOSIM Global $R = 0.117$, $p = 0.001$), shading (ANOSIM Global $R = 0.160$, $p = 0.001$) and tadpole size (ANOSIM Global $R = 0.118$, $p = 0.001$; Figure 10). Pairwise t-tests indicated higher abundances in unshaded mesocosms of oligochaete adults (103.32 ± 9.29 ; $p < 0.001$), oligochaete eggs (23.70 ± 2.31 ; $p = 0.002$), trichopterans (1.24 ± 0.34 ;

$p = 0.044$), and total macroinvertebrates (136.82 ± 10.44 ; $p < 0.001$) relative to shaded mesocosms (48.92 ± 4.44 ; 16.66 ± 2.53 ; 0.30 ± 0.11 ; 74.14 ± 6.65 , respectively).

Nematodes were less abundant in mesocosms with large (0.33 ± 0.12) compared to small tadpoles (2.80 ± 0.91 ; $p = 0.018$). Nematodes and total macroinvertebrates differed in abundance based on the interaction between shading and tadpole size (Table 1). Overall, macroinvertebrates were least abundant in shaded mesocosms with larger tadpoles (Figure 9).

The relative abundances of zooplankton taxa differed by tadpole cage treatment (MANOVA $F_{2,27} = 5.05$, $p < 0.001$; Table 2). Broadly, total zooplankton abundance was lower in mesocosms with free-swimming tadpoles (16.90 ± 5.02) compared to mesocosms with caged tadpoles (33.90 ± 8.25 ; $p = 0.036$) or controls (66.60 ± 6.32 ; $p < 0.001$), and was lower in mesocosms with caged tadpoles compared to controls ($p = 0.011$; Table 2; Figure 11). Copepod nauplii were more abundant in mesocosms with caged tadpoles (29.93 ± 5.38) than those with free-swimming tadpoles (10.30 ± 2.02 ; $p < 0.001$) or controls (12.80 ± 3.19 ; $p = 0.049$), respectively, but did not differ between controls and mesocosms with free-swimming tadpoles ($p = 0.276$). Cladocerans were more abundant in controls (14.20 ± 3.65) compared to mesocosms with free-swimming (6.23 ± 1.57 ; $p = 0.048$) or caged tadpoles (6.03 ± 0.99 ; $p = 0.042$), but did not differ between tadpole treatments ($p = 0.530$). Relative to controls, total zooplankton abundance declined by 49.10% in association with non-consumptive effects of *L. sylvaticus* tadpoles (i.e., caged tadpoles), by 25.52% in association with purely consumptive effects, and by 74.62% in association with consumptive and non-consumptive effects (i.e., uncaged

tadpoles; Figure 11). Among invertebrate taxa, the effects of tadpole predators were more pronounced for zooplankton (Figure 12).

The relative abundance of zooplankton taxa differed by shade status (MANOVA $F_{1,90} = 15.33$, $p < 0.001$). There was also a significant effect of the interaction between tadpole cage treatment and shade status (MANOVA $F_{2,90} = 3.65$, $p = 0.001$). Tadpole size (MANOVA $F_{1,90} = 4.10$, $p = 0.004$), and the interaction between shade status and tadpole size (MANOVA $F_{1,90} = 5.52$, $p = 0.001$; Table 2; Figure 13) also were significant in explaining the variation in zooplankton relative abundance.

Zooplankton community composition did not significantly differ by tadpole cage treatment (ANOSIM Global $R = 0.019$, $p = 0.177$) or tadpole size (ANOSIM Global $R = -0.002$, $p = 0.506$), but was influenced by shading (ANOSIM Global $R = 0.152$, $p = 0.001$; Figure 14). In unshaded mesocosms, cladocerans (10.36 ± 1.66 ; $p = 0.002$), ostracods (13.48 ± 2.48 ; $p < 0.001$), and total zooplankton (45.98 ± 4.33 ; $p = 0.002$) were more abundant compared to shaded mesocosms (5.12 ± 1.28 ; 1.64 ± 0.31 ; 30.00 ± 5.28 , respectively). Additionally, there were fewer cladocerans among large tadpoles (3.55 ± 0.78) compared to small tadpoles (8.70 ± 1.57 ; $p = 0.003$). Copepod nauplii and total zooplankton abundances also differed based on the interaction between cage treatment and shade status, and the interaction between shade status and tadpole size (Table 2). Total zooplankton abundance tended to be lowest in the presence of free-swimming, large tadpoles, and under shaded conditions.

Environmental variables differed among mesocosms based on tadpole cage treatment (MANOVA $F_{2,27} = 5.40$, $p < 0.001$; Table 3). Temperature differed across treatments (ANOVA $p < 0.001$), but Holm's pairwise t-tests indicated no significant

differences between treatments ($p > 0.05$). Biofilm mass was significantly greater in mesocosms with caged (20.52 ± 6.85 mg) compared to free-swimming tadpoles (9.46 ± 2.58 mg; $p = 0.006$), but did not differ between controls (14.97 ± 4.48 mg) and mesocosms with caged ($p = 0.110$) or free-swimming tadpoles ($p = 0.519$). Cage treatment had no influence on relative fluorescence or % dissolved oxygen (Table 3).

Environmental variables differed based on shade status (MANOVA $F_{1,90} = 125.43$, $p < 0.001$), the interaction between tadpole cage treatment and shade status (MANOVA $F_{2,90} = 5.68$, $p < 0.001$), tadpole size (MANOVA $F_{1,90} = 7.42$, $p < 0.001$), and the interaction between tadpole cage treatment and size (MANOVA $F_{2,90} = 3.49$, $p = 0.011$; Table 3). Temperatures were higher in unshaded ($15.54 \pm 0.18^\circ\text{C}$) relative to shaded mesocosms ($12.41 \pm 0.13^\circ\text{C}$; $p < 0.001$), but did not differ based on tadpole size ($p = 0.580$). Biofilm mass did not differ based on habitat shading ($p = 0.740$), but was lower in the presence of large tadpoles (10.18 ± 2.82 mg) compared to small tadpoles (30.87 ± 6.81 mg; $p = 0.015$). Relative fluorescence was lower in unshaded mesocosms (8.19 ± 1.68 RFU) than in shaded mesocosms (16.89 ± 2.27 RFU; $p < 0.001$), and lower in mesocosms containing large (7.79 ± 1.48 RFU) relative to small tadpoles (15.72 ± 2.55 RFU; $p = 0.020$). Dissolved oxygen was also reduced in shaded ($73.93 \pm 1.66\%$) relative to unshaded mesocosms ($101.81 \pm 1.50\%$; $p < 0.001$). The interaction between the treatments of cage and shade level was significant in explaining variation in dissolved oxygen levels and temperature of mesocosms. The interaction between cage treatment and tadpole size was significant in explaining variation in relative fluorescence and dissolved oxygen levels of mesocosms (Table 3).

Due to differing sample sizes among mesocosms, tadpole survival and growth rates by tank ($N = 80$ mesocosms with tadpoles) were analyzed separately from body measurements ($N = 599$ surviving tadpoles) to avoid unbalanced designs. Tadpole survival and growth were collectively not influenced by cage treatment (MANOVA $F_{1,18} = 1.83$, $p = 0.150$) among the mesocosms, but there was a trend of caged tadpoles exhibiting higher rates of survival than free-swimming tadpoles (Table 4). Additionally, neither tadpole body length (ANOVA $F_{1,18} = 0.58$, $p = 0.448$; Table 5), nor head width (ANOVA $F_{1,18} = 0.60$, $p = 0.442$; Table 5) differed based on cage treatment when blocked by ‘mesocosm identity’ as a random effect.

Tadpole survival and growth were affected by shade status (MANOVA $F_{1,72} = 27.84$, $p < 0.001$), size class (MANOVA $F_{1,72} = 28.99$, $p < 0.001$), interactions between tadpole cage treatment and shade status (MANOVA $F_{1,72} = 8.23$, $p < 0.001$), tadpole cage treatment and size class (MANOVA $F_{1,72} = 10.44$, $p < 0.001$), and among all three independent variables (MANOVA $F_{1,72} = 2.88$, $p = 0.042$; Table 4). Although tadpole survival did not differ based on shading ($p = 0.910$), it was higher among large ($89.00 \pm 2.26\%$) compared to small tadpoles ($58.50 \pm 4.45\%$; $p < 0.001$; Figure 15). Average growth rates in length were higher among unshaded (0.64 ± 0.03 mm/day) compared to shaded tadpoles (0.41 ± 0.02 mm/day; $p < 0.001$), but did not differ based on initial tadpole size ($p = 0.170$), whereas growth rates in width were higher among unshaded (0.17 ± 0.01 mm/day) compared to shaded tadpoles (0.11 ± 0.01 mm/day; $p < 0.001$), and among small (0.19 ± 0.01 mm/day) compared to large tadpoles (0.12 ± 0.01 mm/day; $p < 0.001$; Figure 16). Tadpole body lengths also differed based on shade status (ANOVA $F_{1,72} = 26.96$, $p < 0.001$) but not the interaction between tadpole cage and shade

treatments (ANOVA $F_{1,72} = 2.15$, $p = 0.147$; Table 5). On average, unshaded tadpoles grew longer bodies (45.93 ± 0.34 mm) than shaded tadpoles (39.10 ± 0.32 mm; $p < 0.001$; Figure 17). Additionally, tadpole head widths differed based on shade status (ANOVA $F_{1,72} = 55.98$, $p < 0.001$) but not the interaction between tadpole cage and shade treatments (ANOVA $F_{1,72} = 0.16$, $p = 0.735$; Table 5). On average, unshaded tadpoles had wider heads (11.26 ± 0.07 mm) than shaded tadpoles (9.33 ± 0.07 mm; $p < 0.001$).

IV. Discussion

This study demonstrates that *L. sylvaticus* tadpoles feed on invertebrates in natural settings and experimental mesocosms, and elicit consumptive and non-consumptive effects on macroinvertebrate and zooplankton abundance and community composition. Although total macroinvertebrate abundance was not significantly influenced by cage treatment, the reductions in overall zooplankton abundance linked to non-consumptive effects of tadpoles were nearly twice as strong as those linked to consumptive effects, relative to controls. Most tadpoles collected from natural ponds consumed invertebrates, largely zooplankton, indicating that omnivory is a common dietary strategy in this species. Frequencies of tadpole omnivory and abundances of invertebrate groups consumed by tadpoles differed by pond, and larger body sizes facilitated higher frequencies of omnivory. Mesocosm experiments also revealed that predatory effects of tadpoles on invertebrate communities vary by habitat shading and tadpole size. Invertebrate abundance decreased among shaded mesocosms with reduced dissolved oxygen and temperature and in the presence of larger, free-swimming tadpoles, indicating that larger tadpoles likely consume more invertebrates when algae and plant matter are less available. Reduced biofilm masses in mesocosms with large tadpoles suggest that tadpoles may induce stronger limitations on herbivorous invertebrate abundance by limiting food availability, an ontogenetic effect amplified by increased habitat shading. Finally, unshaded tadpoles tended to grow faster and larger, with larger individuals exhibiting greater survivorship, suggesting that shading and aquatic invertebrates (mediated by body size) influence tadpole growth, morphology, and overall fitness.

Lithobates sylvaticus Tadpoles are Primarily Omnivorous

Cases of carnivory or omnivory among tadpoles are taxonomically limited but reveal several key advantages of these foraging strategies. Classic observational studies indicate that some taxa, particularly spadefoot toads, are strict carnivores as tadpoles (Barber and King 1927), and that these and other species engage in conspecific tadpole cannibalism (Bragg 1964, Crump 1986). Reports of omnivory among tadpoles of other species are increasing following the proliferation of stable isotope and fatty acid dietary analytical approaches (reviewed in Montaña *et al.* 2019). Consumption of animal matter in tadpoles may constitute adaptive responses in increasing protein intake, associated developmental rates, and size at metamorphosis (Pfennig 1990, 1992). In tadpoles with morphologies that differ by feeding strategy, carnivorous morphs tend to exhibit greater survival in ephemeral ponds than omnivorous morphs (Pfennig 1992), because increased consumption of high-protein animal matter accelerates growth (Crump 1990) and development (Heinen and Abdella 2005). Metamorphosing anurans that arrive at resources first, and at larger sizes, exhibit greater capacities to exclude competitors (Werner 1986), conferring higher fitness (Semlitsch 1987, Semlitsch *et al.* 1988).

Omnivory in tadpoles is likely an opportunistic feeding strategy which increases in frequency throughout ontogeny. Tadpoles with larger gapes at later developmental stages consume more invertebrate material, whereas smaller, younger tadpoles are typically limited to feeding on algae and detritus (Sousa Filho *et al.* 2007, Schiesari *et al.* 2009). Tadpoles develop relatively wider heads, deeper tails, and smaller gut length:body length ratios during ontogeny, making older tadpoles more efficient predators. Wider

heads facilitate consumption of larger invertebrates (Walls *et al.* 1993, Denoël *et al.* 2006), deeper tails increase speed and maneuverability (Dayton *et al.* 2005), and shorter relative gut lengths process animal material more efficiently (Wickramasinghe *et al.* 2007). In my study, tadpole head width and tail depth were directly related to the likelihood of omnivory, suggesting that gape size and swimming ability are indicative of feeding strategy in *L. sylvaticus*. The lack of a relationship between omnivory and tadpole gut length could be related to the inverse relationship between gut length and temperature (Castaneda *et al.* 2006), as tadpoles in warmer, unshaded habitats tend to develop shorter guts, irrespective of their feeding strategy. Frequencies of omnivory in *L. sylvaticus* tadpoles were likely higher than indicated here, as only the first 10 mm of tadpole guts were excised for gut content analyses. To account for underestimation, 10 tadpoles designated as “non-omnivores” based on the initial analyses had an additional 10 mm of small intestine dissected and examined. Invertebrate material was found in half of these individuals, confirming that estimated proportions of omnivorous tadpoles based on initial analyses represented underestimates, and that *L. sylvaticus* tadpole populations likely engage in more omnivory than suggested here. If tadpoles remained in mesocosms longer prior to dissection, growth of wider gapes would likely have facilitated increased consumption of larger invertebrates (*sensu* Parker 1994, Petranka and Kennedy 1999, Schriever and Williams 2013). The developmental period during which tadpoles consume the most animal material is between Gosner stages 31 – 41 (Gosner 1960, Schriever and Williams 2013). Tadpoles were collected in my study before they reached Gosner stage 42, when forelimbs begin development, as digestive organs prepare for metamorphosis

(Jenssen 1967) and as larval mouthparts atrophy (Gosner 1960), though additional feeding and growth occurs beyond this stage.

Although *L. sylvaticus* tadpoles have comparatively smaller gapes than other omnivorous tadpoles (Schiesari *et al.* 2009), evidence from this and previous studies supports their roles as important predators of aquatic invertebrates. Despite the lower average mass of *L. sylvaticus* tadpoles (2.15 – 2.85 g; Camp *et al.* 1990) compared to larger *L. catesbeianus* tadpoles (6.30 – 9.40 g; Dowe 1979), insects have been reported as the third most consumed food item among *L. sylvaticus* (Schriever and Williams 2013). Stable isotope analyses show that signatures of ^{15}N , indicative of the quantity of animal matter consumed, are similar between omnivorous *L. sylvaticus* tadpoles and wholly carnivorous salamander larvae, whose diets include macroinvertebrates (Schiesari *et al.* 2009). With the exceptions of nematodes, oligochaetes, and chironomids, predation by *L. sylvaticus* tadpoles on macroinvertebrates was limited in this study. Infrequent consumption of larger macroinvertebrates relative to repeated consumption of smaller zooplankton among *L. sylvaticus* tadpoles in ponds is indicative of larval gape-limitations (Schiesari *et al.* 2009). Although *L. sylvaticus* tadpoles were unable to feed frequently on macroinvertebrates, likely due to their relatively small gapes, they may exert similar net predatory effects on invertebrate communities as other larger, less gape-limited amphibian larvae through strong consumptive predatory effects on zooplankton (Rettig *et al.* 2021). Amphibian species with larger larval gapes exert strong impacts on macroinvertebrates, but comparatively weaker impacts on zooplankton (Petranka and Kennedy 1999, Schiesari *et al.* 2009). Given these differences in invertebrate prey, amphibian larvae of different species, and at different sizes, may cause similar reductions

in invertebrate biomass through predation, but via predation on different taxonomic and / or functional groups (Schiesari *et al.* 2009, Rettig *et al.* 2021).

In addition to gape size, hydroperiod also strongly influences frequencies of omnivory among amphibian larvae. Some amphibian larvae consume more animal matter in habitats with longer hydroperiods (Ghioca-Robrecht *et al.* 2009, Kern *et al.* 2013), whereas others engage in more omnivory when occupying highly ephemeral ponds (Pfennig 1992, Hopey and Petranka 1994). Relationships between hydroperiod and frequency of omnivory in amphibian larvae are therefore not uniform across taxa, and whether omnivory increases growth rates or size at metamorphosis depends on the ecological context (Carreira *et al.* 2016, Ramamonjisoa *et al.* 2016). Some amphibians preferentially oviposit in ephemeral ponds because they contain fewer predators of tadpoles (Beranek *et al.* 2021). In such ponds, rates of growth and development by tadpoles are mediated by desiccation risk (Márquez-García *et al.* 2010), and thus tadpoles consuming more protein-rich animal matter develop faster and are more likely to reach metamorphosis prior to desiccation (Heinen and Abdella 2005, Ramamonjisoa *et al.* 2016). In contrast, some amphibians tend to oviposit in ponds with deeper waters and longer hydroperiods, which exhibit lower likelihoods of desiccation (Kern *et al.* 2013), but also support more predators of amphibian larvae (Richter-Boix *et al.* 2007, Amburgey *et al.* 2012). In such habitats, predation risk promotes increased omnivory and subsequent increased size (Crump 1990, Carreira *et al.* 2016) to exceed predator gape limitations. Tadpoles in my study consumed more invertebrates in mesocosms than in ephemeral ponds, and given the lower relative water volume in mesocosms, suggest that frequency of tadpole omnivory was influenced by hydroperiod. Because macroinvertebrate predator

densities were relatively low across all mesocosms, tadpoles were more likely driven to increased omnivory to increase growth rates in these temporary experimental habitats to escape perceived risks of desiccation (Heinen and Abdella 2005, Márquez-García *et al.* 2010, Whiles *et al.* 2010, Ramamonjisoa *et al.* 2016). Whether tadpoles are driven to consume more animal matter in response to threats of desiccation or predation risk, these results broadly suggest that likelihood of tadpole omnivory is influenced either directly or indirectly by hydroperiod in developmental habitats. Future studies should prioritize investigating whether risk of predation or desiccation exert stronger influences on omnivory in tadpoles by simultaneously manipulating hydroperiod and predator presence.

Consumptive and Non-consumptive Effects of Tadpoles on Invertebrates

Consumptive effects, by definition, involve predators eating prey and reducing population sizes whereas non-consumptive effects take various forms and can impact prey morphology, physiology, behavior, and ultimately abundance and life history evolution. Non-consumptive effects of tadpoles often mirror the effects elicited on invertebrates by fish predators. In the absence of direct predation, predatory fish reduce reproductive rates of invertebrates through production of predatory kairomones (Loose and Dawidowicz 1994, McCollum *et al.* 1998), limiting invertebrate recruitment and population sizes. Similar evidence of non-consumptive, kairomone-induced effects of tadpoles on invertebrates are limited to reports of tadpole-conditioned medium stimulating increased zooplankton abundance, (Sarma *et al.* 2011), reproduction, and generation time (Gama-Flores *et al.* 2013). Tadpole predators may also impose non-consumptive effects on invertebrate movement patterns similar to positional changes by

zooplankton in the water column to decrease likelihood of consumption by other predators (Von Elert and Pohnert 2000). Zooplankton may undergo changes in development in response to cues from tadpole predators that are similar to the responses of tadpole prey to predation risks from fish, such as non-lethal predator cues promoting greater body masses in prey that reduce the likelihood of successful predation (Kloskowski 2018). Although direct evidence of non-consumptive effects of tadpole predators are minimal, such impacts on invertebrate abundance, behavior, and development can be indirectly inferred from similar effects elicited from invertebrates by fish (Von Elert and Pohnert 2000) and tadpoles (Kloskowski 2018).

Tadpoles exhibit consumptive and non-consumptive predatory effects on select macroinvertebrate taxa (Whiles *et al.* 2010, Schalk *et al.* 2017, Montaña *et al.* 2019). Despite limited support for non-consumptive effects of tadpole predators, evidence indicates amphibian larvae influence macroinvertebrate populations via transmission of predatory stress hormones (Peacor and Werner 2000, Schoeppner and Relyea 2009), disease transfer (Mokany and Shine 2003b), and reduction in oxygen levels via defecation (Seale 1980, Borges *et al.* 2014). Regardless of mechanism, any consumptive and non-consumptive effects of tadpole predators would be predicted to act in addition to competition between tadpoles and macroinvertebrates (Brönmark *et al.* 1991, Blaustein and Margalit 1994, Mokany and Shine 2003a). In my study, general macroinvertebrate abundance was not influenced by tadpole presence, but for select taxa, free-swimming *L. sylvaticus* tadpoles decreased macroinvertebrate abundances directly via consumption and indirectly, though the specific mechanism of trait-mediated effects were beyond the scope of this study. Although trait-mediated predatory effects on invertebrates are likely,

free-swimming tadpoles exerted greater impacts, relative to controls, on macroinvertebrate abundances than caged tadpoles, indicating stronger consumptive than non-consumptive effects. We did not distinguish whether non-consumptive impacts on macroinvertebrate abundance were due to altered foraging behavior, microhabitat selection, or other mechanisms (Wirsing et al. 2021), and thus results related to non-consumptive effects reflect the net impact of all possible mechanisms. Some macroinvertebrate taxa, such as trichopterans and oligochaete adults and eggs, exhibited reduced abundances in mesocosms with tadpoles, but were not abundant in tadpole guts. Tadpoles likely reduced abundances of such taxa predominantly through non-consumptive effects, such as reductions in oxygen levels from defecation (Borges *et al.* 2014) or transmission of chemical cues that stimulated increased refuge use (Schoeppner and Relyea 2009), indicating that non-consumptive effects of tadpoles alone can alter invertebrate population dynamics. However, given the lack of empirical evidence directly demonstrating suppression of prey abundance via purely non-consumptive effects (Sheriff et al. 2020), future studies employing long-term monitoring of prey while exposed to caged tadpole predators (e.g., *Lithobates catesbeianus*, which overwinter for 2-3 years) would be useful in identifying the mechanisms and severity of suppression.

The impacts of predatory tadpoles on macroinvertebrates extend beyond consumption and non-consumptive predatory effects into other indirect ecological interactions. Macroinvertebrate populations co-occurring with omnivorous tadpole competitors face greater challenges to find algae and plant matter (Brönmark *et al.* 1991, Holomuzki and Hemphill 1996, Atwood and Richardson 2012). In addition to competition, tadpoles may have also indirectly influenced invertebrates through changes

in water temperature. Algae and plants use the enzyme oxidase during cellular respiration, which is linked to heat production (McIntosh 1994). Algal biofilm mass was significantly lower in mesocosms with free-swimming compared to caged tadpoles, and thus consumption of algae by tadpoles may have been responsible for lower average temperatures in this treatment (14.80°C) compared to mesocosms with caged tadpoles (15.00°C) or controls (17.70°C). Cooler waters support fewer macroinvertebrates, particularly non-insects (Hieber *et al.* 2005), and thus tadpoles could have exerted indirect impacts on their abundance via reduced temperatures. Such indirect effects of tadpoles, along with resource competition, would act in concert with impacts of predation to affect abundances of certain macroinvertebrate taxa (Sheriff *et al.* 2020). Although tadpole impacts on macroinvertebrates did not span many taxa, and total abundance was not affected, community composition was still influenced by their presence, indicating that composition can be altered without significant changes in abundances of most taxa in communities (Ghioca-Robrecht and Smith 2011).

Zooplankton communities experience relatively more frequent and / or intense consumptive and non-consumptive predatory effects of tadpoles than macroinvertebrates (Ruibal and Laufer 2012, Caut *et al.* 2013). Amphibian larvae incorporate zooplankton as a major portion of their diets and can selectively target certain taxa to maximize energy gain relative to handling time (Ranta and Nuutinen 1985, Jacobson *et al.* 2017). Reports of non-consumptive effects of tadpoles on zooplankton prey are rare, but generally focus on changes in population dynamics due to chemical cue production (Sarma *et al.* 2011), and responses to these cues may differ among zooplankton taxa (Gama-Flores *et al.* 2013). *Lithobates sylvaticus* tadpoles in my study exerted consumptive and non-

consumptive effects on zooplankton, which mirrors previous studies (Ranta and Nuutinen 1985, Jacobson *et al.* 2017) and indicates that such effects may be relatively common. Non-consumptive effects of tadpoles on zooplankton were 23.58% stronger than consumptive effects, and when combined, reduced overall zooplankton abundance by 74.62%. Despite overall negative non-consumptive effects on zooplankton, copepods were most abundant in mesocosms with caged tadpoles ('B' in Figure 12), indicating positive non-consumptive effects in line with previous studies (Sarma *et al.* 2011, Gama-Flores *et al.* 2013). Although estimated non-consumptive effects cannot be distinguished from simultaneous competitive effects between tadpoles and zooplankton, the presence of zooplankton in tadpole guts indicates that competition was not solely responsible for the effects shown here. Certain zooplankton taxa, such as cladocerans, were abundant in mesocosms lacking tadpoles, exhibited lower abundances in mesocosms with free-swimming tadpoles, and were abundant in tadpole guts, indicating direct consumptive effects (Rettig *et al.* 2021). Tadpoles may target certain zooplankton taxa to increase feeding efficiency (Ranta and Nuutinen 1985, Jacobson *et al.* 2017), or simply forage in microhabitats, or on food sources, also used by zooplankton (Hamilton *et al.* 2012) without exhibiting preference. Zooplankton graze on benthic algae (Balayla and Moss 2004) and periphyton (Masclaux *et al.* 2012) and may have been consumed as bycatch by grazing tadpoles (Sarma *et al.* 2011, Gama-Flores *et al.* 2013). Alternatively, abundance of some zooplankton taxa may have been altered due to non-consumptive impacts of tadpole presence on reproduction (Gama-Flores *et al.* 2013). Tadpoles may therefore serve as important regulators of zooplankton community composition by reducing populations of certain taxa that would otherwise dominate. Although *L. sylvaticus*

tadpoles demonstrated clear predatory effects on zooplankton communities, it remains uncertain whether tadpoles are selectively preying on zooplankton or consuming them unintentionally. Future studies should compare predation rates on zooplankton between tadpoles with different dietary strategies, to determine if herbivorous tadpoles consume similar quantities of zooplankton as omnivorous taxa, indicating incidental consumption.

Effects of Tadpoles on Invertebrates are Linked to Shading and Body Size

Macroinvertebrates generally exhibit lower abundances in shaded habitats (Death and Zimmermann 2005, Schalk *et al.* 2017) with larger predators (Blaustein and Margalit 1996, Dutra and Callisto 2005, Jara 2008). Studies on habitat shading and wetland trophic dynamics support this trend and indicate that habitats with increased canopy coverage have less abundant algae, forming food webs with fewer trophic levels and more intense predation (Jackson *et al.* 2013, Schalk *et al.* 2017). Nearly all macroinvertebrate taxa in this study were less abundant in shaded conditions when in the presence of large tadpoles, and macroinvertebrate community composition differed based on habitat shading, which reflects previous work (Quinn *et al.* 1997, Skelly 2004, Wheeler *et al.* 2007, Schalk *et al.* 2017). Most macroinvertebrates were likely less abundant in shaded conditions due to reduced algal biomass, competition with grazing tadpoles for limited food supplies (Brönmark *et al.* 1991, Blaustein and Margalit 1994, Mokany and Shine 2003a), and increased predation by tadpoles forced to feed on more animal matter (Schalk *et al.* 2017). Some taxa (e.g., oligochaetes) were less abundant in mesocosms with smaller tadpoles, despite tendencies of larger amphibians to predate more macroinvertebrates due to larger gapes. Such invertebrate taxa may have low nutrient

contents (Smith 1985), and because larger tadpoles outcompete smaller conspecifics for prey, smaller individuals may be forced to feed on low-quality invertebrates until they mature (Denoël *et al.* 2006). Future investigations should compare nutrient contents of invertebrate prey consumed across the tadpole size spectrum.

Zooplankton abundance is predicted to decrease during tadpole ontogeny and associated reductions in gape limitations (Carreira *et al.* 2016, Jacobson *et al.* 2017), and under increased canopy coverage if limited primary productivity does not meet the metabolic demands of primary consumers (Hall *et al.* 2007, Lacerot *et al.* 2013). My observations support these predictions; however, habitat shading may also influence consumption of zooplankton indirectly via effects of temperature and light. Higher temperatures under unshaded conditions promote more rapid tadpole growth (Maciel and Juncá 2009), thereby reducing durations in which tadpoles prey on zooplankton. Additionally, increased exposure to UV-B radiation can decrease feeding, and thus growth, in tadpoles due to negative impacts on gene stability and tooth development (Londero *et al.* 2017). Although excessive exposure to UV-B radiation can dampen the ability of tadpoles to act as predators (Londero *et al.* 2017), zooplankton were less abundant in shaded mesocosms with less light exposure and lower temperatures, which is consistent with the hypothesis that tadpoles in cooler waters develop more slowly (Maciel and Juncá 2009), spend longer durations in the presence of invertebrate prey, and consequently cause greater reductions in zooplankton abundance.

Some zooplankton develop defensive structures in response to cues of predation risk (Gilbert 2012). Despite possessing inducible defenses like head spines, these structures grow more slowly and are less effective when zooplankton face larger

predators (Riessen and Trevett-Smith 2009). Cladocerans, which develop defensive head spines and crowns in response to fish predators (Laforsch and Tollrian 2004, Petrusek *et al.* 2009), were least abundant in mesocosms with large tadpoles under shade, and were abundant in tadpole guts. In conjunction with previous data on the susceptibility of zooplankton to predation (Hall *et al.* 2007, Riessen and Trevett-Smith 2009, Lacerot *et al.* 2013), these findings demonstrate two ecological interactions: 1) larger tadpoles represent greater threats to zooplankton with inducible defense mechanisms than smaller conspecifics; and 2) predatory effects of tadpoles on zooplankton are intensified by reduced food availability with increased habitat shading and associated competition. Future studies should involve comparisons of zooplankton that possess or lack inducible defense mechanisms that are consumed by tadpoles across a spectrum of tadpole sizes.

Growth, Morphology, and Survival of Tadpoles are Linked to Invertebrates

Tadpole growth rates are mediated by invertebrate abundance in larval habitats. Tadpoles can reach metamorphosis faster by either consuming animal prey (Crump 1990, Ramamonjisoa *et al.* 2016), or in response to cues from predators (Babbitt and Tanner 1998, Van Buskirk and Yurewicz 1998, Barnett and Richardson 2002). Both mechanisms facilitate more rapid metamorphosis, reducing their likelihood of being consumed by aquatic predators (McIntyre *et al.* 2004) and enhancing their ability to secure terrestrial resources before competitors (Werner 1986, Semlitsch 1987, Semlitsch *et al.* 1988). In my study, tadpoles grew faster in unshaded mesocosms, which contained more zooplankton and macroinvertebrates, suggesting invertebrate abundance is directly related to tadpole growth. Tadpoles likely grew faster in mesocosms with more

invertebrates due to increased protein availability, rather than in response to cues of predation risk, because predatory macroinvertebrates were relatively rare.

The physiological responses of tadpoles to invertebrates are mediated by degree of habitat shading. Sufficient supplies of Vitamin D, which can be synthesized by amphibians via sunlight exposure, are necessary for the metabolism of calcium (Michaels *et al.* 2015). Tadpoles developing in shaded conditions may experience Vitamin D deficiencies associated with reduced calcium supplies, and resultant developmental abnormalities that reduce fitness (Antwis and Browne 2009, Camperio Ciani *et al.* 2018). Given these requirements, tadpoles with sufficient light exposure would be less prone to developmental abnormalities (Michaels *et al.* 2015, Camperio Ciani *et al.* 2018), would have increased ability to prey on invertebrates (Antwis and Browne 2009, Schiesari *et al.* 2009), and would reach larger sizes, grow faster (Crump 1990), and achieve higher overall fitness. In unshaded mesocosms, larger tadpoles achieve greater survivorship (Beachy 1995, Newman 1998, Maciel and Juncá 2009, Dastansara *et al.* 2017), potentially because of their greater capacity to predate invertebrates, coupled with increased sunlight availability supporting proper development. Although smaller tadpoles in unshaded tanks exhibited lower survivorship, they exhibited faster growth rates. Smaller, unshaded tadpoles may have grown faster because of abundant sunlight coupled with pressures to quickly reach larger sizes conducive to expanding their dietary breadth and increasing fitness. These differences in growth rates indicate non-linear patterns of attenuated growth during ontogeny observed in previous studies (Werner 1986) and suggest that both food (e.g., invertebrates) and better environmental conditions (e.g.,

sunlight exposure) are crucial components in tadpole survival (Martins *et al.* 2013) and development (Maciel and Juncá 2009).

Given their roles in shaping aquatic invertebrate communities in temperate ecosystems (Regeister *et al.* 2006, Bowatte *et al.* 2013, Montaña *et al.* 2019), further reductions in amphibian abundance and species richness could have severe ecological consequences. Larval amphibians serve essential ecosystem functions in aquatic habitats, ranging from controlling invertebrate populations via predatory effects (Schiesari *et al.* 2009, Whiles *et al.* 2010, Bowatte *et al.* 2013) to bioturbation that opens feeding grounds for algae-eating taxa (Ranvestel *et al.* 2004). Additional reductions in amphibian abundance and diversity could cause changes in algal densities that create bottom-up trophic cascades and destabilize aquatic ecosystems (Whiles *et al.* 2006). Regardless of how larval amphibians influence aquatic ecosystems, future studies should investigate how tadpole presence impacts the relative abundance of taxa at each trophic level, to better predict how food web structure may change with continued population declines.

List of References

- Altig, R., and J. P. Kelly. 1974. Indices of feeding in anuran tadpoles as indicated by gut characteristics. *Herpetologica* 30:200-203.
- Altig, R., M. R. Whiles, and C. L. Taylor. 2007. What do tadpoles really eat? Assessing the trophic status of an unstudied and imperiled group of consumers in freshwater habitats. *Freshwater Biology* 52:386-395.
- Amburgey, S., W. C. Funk, M. Murphy, and E. Muths. 2012. Effects of hydroperiod duration on survival, developmental rate, and size at metamorphosis in boreal chorus frog tadpoles (*Pseudacris maculata*). *Herpetologica* 68:456-467.
- Antwis, R. E., and R. K. Browne. 2009. Ultraviolet radiation and Vitamin D3 in amphibian health, behaviour, diet and conservation. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 154:184-190.
- Aspbury, A. S., and S. A. Juliano. 1998. Negative effects of habitat drying and prior exploitation on the detritus resource in an ephemeral aquatic habitat. *Oecologia* 115:137-148.
- Atwood, T., and J. S. Richardson. 2012. Trophic interactions between insects and stream-associated amphibians in steep, cobble-bottom streams of the Pacific Coast of North America. *Insects* 3:432-441.
- Babbitt, K. J., and G. W. Tanner. 1998. Effects of cover and predator size on survival and development of *Rana utricularia* tadpoles. *Oecologia* 114:258-262.
- Balayla, D. J., and B. Moss. 2004. Relative importance of grazing on algae by plant-associated and open-water microcrustacea (Cladocera). *Archiv fur Hydrobiologie* 161:199-224.
- Barber, M. A., and C. H. King. 1927. The tadpole of the spadefoot toad an enemy of mosquito larvae. *Public Health Reports (1896-1970)*:3189-3193.
- Barnett, H. K., and J. S. Richardson. 2002. Predation risk and competition effects on the life-history characteristics of larval Oregon spotted frog and larval red-legged frog. *Oecologia* 132:436-444.
- Beachy, C. K. 1995. Effects of larval growth history on metamorphosis in a stream-dwelling salamander (*Desmognathus ochrophaeus*). *Journal of Herpetology* 29:375-382.
- Benard, M. F. 2004. Predator-induced phenotypic plasticity in organisms with complex life histories. *Annu. Rev. Ecol. Evol. Syst.* 35:651-673.
- Beranek, C. T., S. Sanders, J. Clulow, and M. Mahony. 2021. Predator-free short-hydroperiod wetlands enhance metamorph output in a threatened amphibian: insights into frog breeding behaviour evolution and conservation management. *Wildlife Research*. <https://doi.org/10.1071/WR21049>
- Berven, K. A. 1982. The genetic basis of altitudinal variation in the wood frog *Rana sylvatica*. An experimental analysis of life history traits. *Evolution* 71:962-983.

- Biesterfeldt, J. M., J. W. Petranka, and S. Sherbondy. 1993. Prevalence of chemical interference competition in natural populations of wood frogs, *Rana sylvatica*. *Copeia* 1993:688-695.
- Bishop, P. J., A. Angulo, J. P. Lewis, R. D. Moore, G. B. Rabb, and J. G. Moreno. 2012. The Amphibian Extinction Crisis-what will it take to put the action into the Amphibian Conservation Action Plan? *SAPIENS* 5:97-111.
- Blaustein, A. R., A. Hatch, L. K. Belden, and E. L. Wildy. 2001. Influence of abiotic and biotic factors on amphibians in ephemeral ponds with special reference to long-toed salamanders (*Ambystoma macrodactylum*). *Israel Journal of Zoology* 47:333-346.
- Blaustein, L., and J. Margalit. 1996. Priority effects in temporary pools: nature and outcome of mosquito larva-toad tadpole interactions depend on order of entrance. *Journal of Animal Ecology* 65:77-84.
- Blaustein, L., and J. Margalit. 1994. Mosquito larvae (*Culiseta longiareolata*) prey upon and compete with toad tadpoles (*Bufo viridis*). *Journal of Animal Ecology* 63:841-850.
- Borges, F. D. F., M. V. D. Stéfani, and L. A. D. Amaral. 2014. Quality of the effluents of bullfrog tadpole ponds. *Boletim Do Instituto de Pesca* 40:409-417.
- Boulton, A. J., L. Boyero, A. P. Covich, M. Dobson, S. Lake, and R. Pearson. 2008. Are tropical streams ecologically different from temperate streams? *Tropical Stream Ecology* 2008:257-284.
- Bowatte, G., P. Perera, G. Senevirathne, S. Meegaskumbura, and M. Meegaskumbura. 2013. Tadpoles as dengue mosquito (*Aedes aegypti*) egg predators. *Biological Control* 67:469-474.
- Bragg, A. N. 1964. Further study of predation and cannibalism in spadefoot tadpoles. *Herpetologica* 20:17-24.
- Brönmark, C., S. D. Rundle, and A. Erlandsson. 1991. Interactions between freshwater snails and tadpoles: competition and facilitation. *Oecologia* 87:8-18.
- Camp, C. D., C. E. Condee, and G. Lovell. 1990. Oviposition, larval development and metamorphosis in the wood frog, *Rana sylvatica* (Anura: Ranidae) in Georgia. *Brimleyana* 16:17-21.
- Camperio Ciani, J. F., J. Guerrel, E. Baitchman, R. Diaz, M. Evans, R. Ibáñez, H. Ross, E. Klaphake, B. Nissen, A. P. Pessier, M. L. Power, C. Arlotta, D. Snellgrove, B. Wilson, and B. Gratwicke. 2018. The relationship between spindly leg syndrome incidence and water composition, overfeeding, and diet in newly metamorphosed harlequin frogs (*Atelopus* spp.). *PloS one* 13:e0204314.
- Carreira, B. M., P. Segurado, G. Orizaola, N. Gonçalves, V. Pinto, A. Laurila, and R. Rebelo. 2016. Warm vegetarians? Heat waves and diet shifts in tadpoles. *Ecology* 97:2964-2974.
- Castaneda, L. E., P. Sabat, S. P. Gonzalez, and R. F. Nespolo. 2006. Digestive plasticity in tadpoles of the Chilean giant frog (*Caudiverbera caudiverbera*): factorial

- effects of diet and temperature. *Physiological and Biochemical Zoology* 79:919-926.
- Caut, S., E. Angulo, C. Díaz-Paniagua, and I. Gomez-Mestre. 2013. Plastic changes in tadpole trophic ecology revealed by stable isotope analysis. *Oecologia* 173:95-105.
- Chalcraft, D. R., and W. J. Resetarits Jr. 2003. Predator identity and ecological impacts: functional redundancy or functional diversity? *Ecology* 84:2407-2418.
- Connell, S. D. 1998. Effects of predators on growth, mortality and abundance of a juvenile reef-fish: evidence from manipulations of predator and prey abundance. *Marine Ecology Progress Series* 169:251-261.
- Corn, P. S., and L. J. Livo. 1989. Leopard frog and wood frog reproduction in Colorado and Wyoming. *Northwestern Naturalist* 70:1-9.
- Crump, M. L. 1990. Possible enhancement of growth in tadpoles through cannibalism. *Copeia* 1990:560-564.
- Crump, M. L. 1986. Cannibalism by younger tadpoles: another hazard of metamorphosis. *Copeia* 1986:1007-1009.
- Dastansara, N., S. Vaissi, J. Mosavi, and M. Sharifi. 2017. Impacts of temperature on growth, development and survival of larval *Bufo (Pseudepidalea) viridis* (Amphibia: Anura): implications of climate change. *Zoology and Ecology* 27:228-234.
- Dayton, G. H., D. Saenz, K. A. Baum, R. B. Langerhans, and T. J. DeWitt. 2005. Body shape, burst speed and escape behavior of larval anurans. *Oikos* 111:582-591.
- Death, R. G., and E. M. Zimmermann. 2005. Interaction between disturbance and primary productivity in determining stream invertebrate diversity. *Oikos* 111:392-402.
- Denoël, M., H. H. Whiteman., and S. A. Wissinger. 2006. Temporal shift of diet in alternative cannibalistic morphs of the tiger salamander. *Biological Journal of the Linnean Society* 89:373-382.
- Dillard, G. E. 1999. Common freshwater algae of the United States: An illustrated key to the genera (excluding the diatoms). Berlin: J. Cramer.
- do Amaral, D. F., M. F. Montalvão, B. de Oliveira Mendes, A. L. da Silva Castro, and G. Malafaia. 2018. Behavioral and mutagenic biomarkers in tadpoles exposed to different abamectin concentrations. *Environmental Science and Pollution Research* 25:12932-12946.
- Dowe, B. J. 1979. The effect of time of oviposition and microenvironment on growth of larval bullfrogs (*Rana catesbeiana*) in Arizona. M.S. thesis, Arizona State University, Tempe.
- Dutra, S. L., and M. Callisto. 2005. Macroinvertebrates as tadpole food: importance and body size relationships. *Revista Brasileira de Zoologia* 22:923-927.

- Eaton, B. R., and C. A. Paszkowski. 1999. *Rana sylvatica* (wood frog). Predation. *Herpetological Review* 30:164.
- Gallagher, S. J., B. J. Tornabene, T. S. DeBlieux, K. M. Pochini, M. F. Chislock, Z. A. Compton, L. K. Eiler, K. M. Verble, and J. T. Hoverman. 2019. Healthy but smaller herds: Predators reduce pathogen transmission in an amphibian assemblage. *Journal of Animal Ecology* 88:1613-1624.
- Gama-Flores, J. L., M. E. Huidobro-Salas, S. S. S. Sarma, and S. Nandini. 2013. Effects of allelochemicals released by vertebrates (fish, salamander and tadpole) on *Moina macrocopa* (Cladocera). *Allelopathy Journal* 31:415-425.
- Ghioca-Robrecht, D. M., and L. M. Smith. 2011. The role of Spadefoot Toad tadpoles in wetland trophic structure as influenced by environmental and morphological factors. *Canadian Journal of Zoology* 89:47-59.
- Ghioca-Robrecht, D. M., L. M. Smith, and L. D. Densmore. 2009. Ecological correlates of trophic polyphenism in spadefoot tadpoles inhabiting playas. *Canadian Journal of Zoology* 87:229-238.
- Gilbert, J. J. 2012. Effects of an ostracod (*Cypris pubera*) on the rotifer *Keratella tropica*: predation and reduced spine development. *International Review of Hydrobiology* 97:445-453.
- Gosner, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16:183-190.
- Hall, E. M., C. S. Goldberg, J. L. Brunner, and E. J. Crespi. 2018. Seasonal dynamics and potential drivers of ranavirus epidemics in wood frog populations. *Oecologia* 188:1253-1262.
- Hall, S. R., M. A. Leibold, D. A. Lytle, and V. H. Smith. 2007. Grazers, producer stoichiometry, and the light: nutrient hypothesis revisited. *Ecology* 88:1142-1152.
- Hamilton, P. T., J. M. Richardson, and B. R. Anholt. 2012. *Daphnia* in tadpole mesocosms: trophic links and interactions with *Batrachochytrium dendrobatidis*. *Freshwater Biology* 57:676-683.
- Hecnar, S. J., and R. T. M'Closkey. 1997. The effects of predatory fish on amphibian species richness and distribution. *Biological Conservation* 79:123-131.
- Heinen, J. T., and J. A. Abdella. 2005. On the advantages of putative cannibalism in American toad tadpoles (*Bufo a. americanus*): is it active or passive and why? *The American Midland Naturalist* 153:338-347.
- Heins, D. C., H. Knoper, and J. A. Baker. 2016. Consumptive and non-consumptive effects of predation by introduced northern pike on life-history traits in threespine stickleback. *Evolutionary Ecology Research* 17:355-372.
- Helsel, D. R., S. A. Archfield, E. J. Gilroy, K. R. Ryberg, and R. M. Hirsch. 2020. *Statistical methods in water resources*. U.S. Department of the Interior, U.S. Geological Survey.

- Hieber, M., C. T. Robinson, U. R. S. Uehlinger, and J. V. Ward. 2005. A comparison of benthic macroinvertebrate assemblages among different types of alpine streams. *Freshwater Biology* 50:2087-2100.
- Hite, J. L., M. C. Hughey, K. M. Warkentin, and J. R. Vonesh. 2018. Cross-ecosystem effects of terrestrial predators link treefrogs, zooplankton, and aquatic primary production. *Ecosphere* 9:1-14.
- Holomuzki, J. R. 1998. Grazing effects by green frog tadpoles (*Rana clamitans*) in a woodland pond. *Journal of Freshwater Ecology* 13:1-8.
- Holomuzki, J. R., and N. Hemphill. 1996. Snail-tadpole interactions in streamside pools. *The American Midland Naturalist* 136:315-327.
- Hopey, M. E., and J. W. Petranka. 1994. Restriction of wood frogs to fish-free habitats: how important is adult choice? *Copeia* 1994:1023-1025.
- Jackson, A. T., A. Adite, K. A. Roach, and K. O. Winemiller. 2013. Primary production, food web structure, and fish yields in constructed and natural wetlands in the floodplain of an African river. *Canadian Journal of Fisheries and Aquatic Sciences* 70:543-553.
- Jacobson, B. J., A. Cervantes-Martínez, and M. A. Gutiérrez-Aguirre. 2017. Selectivity of *Incilius valliceps* (Anura: Bufonidae) tadpoles on freshwater zooplankton. *Hidrobiológica* 27:211-217.
- Jara, F. G. 2008. Tadpole–odonate larvae interactions: influence of body size and diel rhythm. *Aquatic Ecology* 42:503-509.
- Jefferson, D. M., K. A. Hobson, B. S. Demuth, M. C. Ferrari, and D. P. Chivers. 2014. Frugal cannibals: how consuming conspecific tissues can provide conditional benefits to wood frog tadpoles (*Lithobates sylvaticus*). *Naturwissenschaften* 101:291-303.
- Jenssen, T. A. 1967. Food habits of the green frog, *Rana clamitans*, before and during metamorphosis. *Copeia* 1967:214-218.
- Jordan, F., M. Bartolini, C. Nelson, P. E. Patterson, and H. L. Soulen. 1997. Risk of predation affects habitat selection by the pinfish *Lagodon rhomboides* (Linnaeus). *Journal of Experimental Marine Biology and Ecology* 208:45-56.
- Juanes, F., and D. O. Conover. 1995. Size-structured piscivory: advection and the linkage between predator and prey recruitment in young-of-the-year bluefish. *Marine Ecology Progress Series* 128:287-304.
- Kern, M. M., A. A. Nassar, J. C. Guzy, and M. E. Dorcas. 2013. Oviposition site selection by spotted salamanders (*Ambystoma maculatum*) in an isolated wetland. *Journal of Herpetology* 47:445-449.
- Kindinger, T. L., and M. A. Albins. 2017. Consumptive and non-consumptive effects of an invasive marine predator on native coral-reef herbivores. *Biological Invasions* 19:131-146.
- Kloskowski, J. 2018. Total non-consumptive effects of fish on *Pelobates fuscus* and *Hyla orientalis* tadpoles in pond enclosure experiments. *Zoological Science* 35:528-534.

- Kupferberg, S. 1997. Facilitation of periphyton production by tadpole grazing: functional differences between species. *Freshwater Biology* 37:427-439.
- Lacerot, G., C. Kruk, M. Lüring, and M. Scheffer. 2013. The role of subtropical zooplankton as grazers of phytoplankton under different predation levels. *Freshwater Biology* 58:494-503.
- Laforsch, C., and R. Tollrian. 2004. Inducible defenses in multipredator environments: cyclomorphosis in *Daphnia cucullata*. *Ecology* 85:2302-2311.
- Leff, L. G., and M. D. Bachmann. 1986. Ontogenetic changes in predatory behavior of larval tiger salamanders (*Ambystoma tigrinum*). *Canadian Journal of Zoology* 64:1337-1344.
- Levis, N. A., S. de la Serna Buzón, and D. W. Pfennig. 2015. An inducible offense: carnivore morph tadpoles induced by tadpole carnivory. *Ecology and Evolution* 5:1405-1411.
- Londero, J. E. L., C. P. Dos Santos, A. L. A. Segatto, and A. P. Schuch. 2017. Impacts of UVB radiation on food consumption of forest specialist tadpoles. *Ecotoxicology and Environmental Safety* 143:12-18.
- Loose, C. J., and P. Dawidowicz. 1994. Trade-offs in diel vertical migration by zooplankton: the costs of predator avoidance. *Ecology* 75:2255-2263.
- Maciel, T. A., and F. A. Juncá. 2009. Effects of temperature and volume of water on the growth and development of tadpoles of *Pleurodema diplolister* and *Rhinella granulosa* (Amphibia: Anura). *Zoologia (Curitiba)* 26:413-418.
- Magoulick, D. D. 2004. Effects of predation risk on habitat selection by water column fish, benthic fish and crayfish in stream pools. *Hydrobiologia* 527:209-221.
- Maher, J. M., E. E. Werner, and R. J. Denver. 2013. Stress hormones mediate predator-induced phenotypic plasticity in amphibian tadpoles. *Proceedings of the Royal Society B* 280:1-9.
- Mallory, M. A., and J. S. Richardson. 2005. Complex interactions of light, nutrients and consumer density in a stream periphyton-grazer (tailed frog tadpoles) system. *Journal of Animal Ecology* 74:1020-1028.
- Márquez-García, M., M. Correa-Solís, and M. A. Méndez. 2010. Life-history trait variation in tadpoles of the warty toad in response to pond drying. *Journal of Zoology* 281:105-111.
- Martin, T. H., L. B. Crowder, C. F. Dumas, and J. M. Burkholder. 1992. Indirect effects of fish on macrophytes in Bays Mountain Lake: evidence for a littoral trophic cascade. *Oecologia* 89:476-481.
- Martins, F. M., M. D. M. Oom, R. Rebelo, and G. M. Rosa. 2013. Differential effects of dietary protein on early life-history and morphological traits in natterjack toad (*Epidalea calamita*) tadpoles reared in captivity. *Zoo Biology* 32:457-462.
- Martof, B. S., and R. L. Humphries. 1959. Geographic variation in the wood frog *Rana sylvatica*. *The American Midland Naturalist* 61:350-389.

- Masclaux, H., A. Bec, and G. Bourdier. 2012. Trophic partitioning among three littoral microcrustaceans: relative importance of periphyton as food resource. *Journal of Limnology* 71:261-266.
- McCollum, E. W., L. B. Crowder, and S. A. McCollum. 1998. Complex interactions of fish, snails, and littoral zone periphyton. *Ecology* 79:1980-1994.
- McCollum, S. A., and J. D. Leimberger. 1997. Predator-induced morphological changes in an amphibian: predation by dragonflies affects tadpole shape and color. *Oecologia* 109:615-621.
- McCollum, S. A., and J. Van Buskirk. 1996. Costs and benefits of a predator-induced polyphenism in the gray treefrog *Hyla chrysoscelis*. *Evolution* 50:583-593.
- McIntosh, L. 1994. Molecular biology of the alternative oxidase. *Plant Physiology* 105:781.
- McIntyre, P. B., S. Baldwin, and A. S. Flecker. 2004. Effects of behavioral and morphological plasticity on risk of predation in a Neotropical tadpole. *Oecologia* 141:130-138.
- Medina, R., G. O. Wogan, K. Bi, F. Termignoni-García, M. H. Bernal, J. P. Jaramillo-Correa, I. J. Wang, and E. Vázquez-Domínguez. 2021. Phenotypic and genomic diversification with isolation by environment along elevational gradients in a neotropical treefrog. *Molecular Ecology* 30:4062-4076.
- Merritt, R. W., and K. W. Cummins (Eds.). 1996. An introduction to the aquatic insects of North America. 3rd ed. Kendall Hunt Publishing Company, Dubuque, IA, USA.
- Michaels, C. J., R. E. Antwis, and R. F. Preziosi. 2015. Impacts of UVB provision and dietary calcium content on serum vitamin D3, growth rates, skeletal structure and coloration in captive oriental fire-bellied toads (*Bombina orientalis*). *Journal of Animal Physiology and Animal Nutrition* 99:391-403.
- Mokany, A., and R. Shine. 2003a. Competition between tadpoles and mosquito larvae. *Oecologia* 135:615-620.
- Mokany, A., and R. Shine. 2003b. Biological warfare in the garden pond: tadpoles suppress the growth of mosquito larvae. *Ecological Entomology* 28:102-108.
- Montaña, C. G., S. D. G. T. M. Silva, D. Hagyari, J. Wager, L. Tiegs, C. Sadeghian, T. A Schriever, and C. M. Schalk. 2019. Revisiting “what do tadpoles really eat?” A 10-year perspective. *Freshwater Biology* 64:2269-2282.
- Newman, R. A. 1998. Ecological constraints on amphibian metamorphosis: interactions of temperature and larval density with responses to changing food level. *Oecologia* 115:9-16.
- Ocock, J. F., K. J. Brandis, B. J. Wolfenden, K. M. Jenkins, and S. Wassens. 2019. Gut content and stable isotope analysis of tadpoles in floodplain wetlands. *Australian Journal of Zoology* 66:261-271.
- Parker, M. S. 1994. Feeding ecology of stream-dwelling Pacific giant salamander larvae (*Dicamptodon tenebrosus*). *Copeia* 1994:705-718.
- Peacor, S. D., and E. E. Werner. 2000. Predator effects on an assemblage of consumers through induced changes in consumer foraging behavior. *Ecology* 81:1998-2010.

- Perez, A., M. J. Mazerolle, and J. Brisson. 2013. Effects of exotic common reed (*Phragmites australis*) on wood frog (*Lithobates sylvaticus*) tadpole growth and food availability. *Journal of Freshwater Ecology* 28:165-177.
- Pessarrodona, A., J. Boada, J. F. Pagès, R. Arthur, and T. Alcoverro. 2019. Consumptive and non-consumptive effects of predators vary with the ontogeny of their prey. *Ecology* 100:1-13.
- Petranka, J. W., and C. A. Kennedy. 1999. Pond tadpoles with generalized morphology: is it time to reconsider their functional roles in aquatic communities? *Oecologia* 120:621-631.
- Petranka, J. W., and D. A. Thomas. 1995. Explosive breeding reduces egg and tadpole cannibalism in the wood frog, *Rana sylvatica*. *Animal Behaviour* 50:731-739.
- Petranka, J. W., M. E. Hopey, B. T. Jennings, S. D. Baird, and S. J. Boone. 1994. Breeding habitat segregation of wood frogs and American toads: the role of interspecific tadpole predation and adult choice. *Copeia* 1994:691-697.
- Petrusek, A., R. Tollrian, K. Schwenk, A. Haas, and C. Laforsch. 2009. A “crown of thorns” is an inducible defense that protects *Daphnia* against an ancient predator. *Proceedings of the National Academy of Sciences* 106:2248-2252.
- Pfennig, D. W. 1999. Cannibalistic tadpoles that pose the greatest threat to kin are most likely to discriminate kin. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 266:57-61.
- Pfennig, D. W. 1992. Polyphenism in spadefoot toad tadpoles as a locally adjusted evolutionarily stable strategy. *Evolution* 46:1408-1420.
- Pfennig, D. W. 1990. The adaptive significance of an environmentally-cued developmental switch in an anuran tadpole. *Oecologia* 85:101-107.
- Preisser, E. L., D. I. Bolnick, and J. H. Grabowski. 2009. Resource dynamics influence the strength of non-consumptive predator effects on prey. *Ecology Letters* 12:315-323.
- Prevosti, F. J., A. Forasiepi, and N. Zimicz. 2013. The evolution of the Cenozoic terrestrial mammalian predator guild in South America: competition or replacement? *Journal of Mammalian Evolution* 20:3-21.
- Quinn, J. M., A. B. Cooper, M. J. Stroud, and G. P. Burrell. 1997. Shade effects on stream periphyton and invertebrates: an experiment in streamside channels. *New Zealand Journal of Marine and Freshwater Research* 31:665-683.
- Ramamonjisoa, N., N. Iwai, and Y. Natuhara. 2016. Post-metamorphic costs of carnivorous diets in an omnivorous tadpole. *Copeia* 104:808-815.
- Ranta, E., and V. Nuutinen. 1985. Foraging by the smooth newt (*Triturus vulgaris*) on zooplankton: functional responses and diet choice. *The Journal of Animal Ecology* 54:275-293.
- Ranvestel, A. W., K. R. Lips, C. M. Pringle, M. R. Whiles, and R. J. Bixby. 2004. Neotropical tadpoles influence stream benthos: evidence for the ecological

- consequences of decline in amphibian populations. *Freshwater Biology* 49:274-285.
- R Core Team. 2018. R: A language and environment for statistical computing.
- Redmer, M., and S. E. Trauth. 2005. *Rana sylvatica* LeConte, 1825, wood frog. Amphibian declines: the conservation status of United States species. Edited by M. Lannoo. University of California Press, Berkeley and Los Angeles 2005:590-593.
- Redmer, M. 2002. Natural history of the wood frog (*Rana sylvatica*) in the Shawnee National Forest, southern Illinois. *Illinois Natural History Survey Bulletin* 36:163-194.
- Register, K. J., M. R. Whiles, and K. R. Lips. 2008. Variation in the trophic basis of production and energy flow associated with emergence of larval salamander assemblages from forest ponds. *Freshwater Biology* 53:1754-1767.
- Register, 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.
- Relyea, R. A. 2002. Local population differences in phenotypic plasticity: predator-induced changes in wood frog tadpoles. *Ecological Monographs* 72:77-93.
- Rettig, J. E., N. R. Teeters, and G. R. Smith. 2021. Effects of the Interaction of Bluegill and Two Species of Tadpoles on Experimental Zooplankton Communities. *The American Midland Naturalist* 186:95-105.
- Richter-Boix, A., G. A. Llorente, and A. Montori. 2007. A comparative study of predator-induced phenotype in tadpoles across a pond permanency gradient. *Hydrobiologia* 583:43-56.
- Riessen, H. P., and J. B. Trevett-Smith. 2009. Turning inducible defenses on and off: adaptive responses of *Daphnia* to a gape-limited predator. *Ecology* 90:3455-3469.
- Rueden, C. T., J. Schindelin, and M. C. Hiner. 2017. ImageJ2: ImageJ for the next generation of scientific image data. *BMC Bioinformatics* 18:529.
- Ruibal, M., and G. Laufer. 2012. Bullfrog *Lithobates catesbeianus* (Amphibia: Ranidae) tadpole diet: description and analysis for three invasive populations in Uruguay. *Amphibia-Reptilia* 33:355-363.
- Sarma, S. S. S., G. C. Gómez-Cabral, A. García-Arroyo, and S. Nandini. 2011. Effects of kairomones from predatory vertebrates on the population growth of rotifer *Platyonus patulus* (Müller). *Allelopathy Journal* 27:301-308.
- Say-Sallaz, E., S. Chamailé-Jammes, H. Fritz, and M. Valeix. 2019. Non-consumptive effects of predation in large terrestrial mammals: Mapping our knowledge and revealing the tip of the iceberg. *Biological Conservation* 235:36-52.
- Schalk, C. M., C. G. Montaña, K. O. Winemiller, and L. A. Fitzgerald. 2017. Trophic plasticity, environmental gradients and food-web structure of tropical pond communities. *Freshwater Biology* 62:519-529.

- Scheiner, S. M. 1993. MANOVA: Multiple Response Variables and Multispecies Interactions (eds. S.M. Scheiner and J. Gurevitch). Chapman and Hall, New York, New York, USA.
- 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.
- Schoeppner, N. M., and R. A. Relyea. 2009. Interpreting the smells of predation: how alarm cues and kairomones induce different prey defences. *Functional Ecology* 23:1114-1121.
- Schriever, T. A., and D. D. Williams. 2013. Ontogenetic and individual diet variation in amphibian larvae across an environmental gradient. *Freshwater Biology* 58:223-236.
- Seale, D. B. 1980. Influence of amphibian larvae on primary production, nutrient flux, and competition in a pond ecosystem. *Ecology* 61:1531-1550.
- Seigel, R. A. 1983. Natural survival of eggs and tadpoles of the wood frog, *Rana sylvatica*. *Copeia* 1983:1096-1098.
- Semlitsch, R. D. 1987. Density-dependent growth and fecundity in the paedomorphic salamander *Ambystoma talpoideum*. *Ecology* 68:1003-1008.
- Semlitsch, R. D., D. E. Scott, and J. H. Pechmann. 1988. Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. *Ecology* 69:184-192.
- Sheriff, M. J., S. D. Peacor, D. Hawlena, and M. Thaker. 2020. Non-consumptive predator effects on prey population size: A dearth of evidence. *Journal of Animal Ecology* 89:1302-1316.
- Shurin, J. B. 2001. Interactive effects of predation and dispersal on zooplankton communities. *Ecology* 82:3404-3416.
- Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters* 5:785-791.
- Skelly, D. K. 2004. Microgeographic countergradient variation in the wood frog, *Rana sylvatica*. *Evolution* 58:160-165.
- Skelly, D. K., and E. E. Werner. 1990. Behavioral and life-historical responses of larval American toads to an odonate predator. *Ecology* 71:2312-2322.
- Smith, D. G. 2001. Pennak's freshwater invertebrates of the United States: Porifera to Crustacea, 4th ed. Wiley, New York, New York, USA.
- Smith, D. S. 2019. Ecosystem functional consequences of body size variation in an apex predator (*Ambystoma jeffersonianum*). M.S. Thesis, Eastern Kentucky University, Richmond, Kentucky, USA.
- Smith, M. E. 1985. Tubificid worms: important organisms in aquatic ecosystems. *The American Biology Teacher* 47:412-415.

- Sours, G. N., and J. W. Petranka. 2007. Intraguild predation and competition mediate stage-structured interactions between wood frog (*Rana sylvatica*) and upland chorus frog (*Pseudacris feriarum*) larvae. *Copeia* 2007:131-139.
- Sousa Filho, I. F. D., C. C. Branco, A. M. Carvalho-e-Silva, G. R. D. Silva, and L. T. Sabagh. 2007. The diet of *Scinax angnensis* (Lutz) tadpoles in an area of the Atlantic Forest (Mangaratiba, Rio de Janeiro) (Amphibia, Anura, Hylidae). *Revista Brasileira de Zoologia* 24:965-970.
- Steiner, U. K. 2007. Linking antipredator behaviour, ingestion, gut evacuation and costs of predator-induced responses in tadpoles. *Animal Behaviour* 74:1473-1479.
- Strobbe, F., M. A. McPeck, M. De Block, and R. Stoks. 2011. Fish predation selects for reduced foraging activity. *Behavioral Ecology and Sociobiology* 65:241-247.
- Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. Rodrigues, D. L. Fischman, and R. W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* 306:1783-1786.
- Thorp, J. H., and M. L. Cothran. 1984. Regulation of freshwater community structure at multiple intensities of dragonfly predation. *Ecology* 65:1546-1555.
- Toledo, L. F., and C. F. Haddad. 2009. Colors and some morphological traits as defensive mechanisms in anurans. *International Journal of Zoology* 2009:1-12.
- Van Buskirk, J., and K. L. Yurewicz. 1998. Effects of predators on prey growth rate: relative contributions of thinning and reduced activity. *Oikos* 82:20-28.
- Vitousek, P. M., and R. L. Sanford. 1986. Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics* 17:137-167.
- Vitousek, P. M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65:285-298.
- Von Elert, E., and G. Pohnert. 2000. Predator specificity of kairomones in diel vertical migration of *Daphnia*: a chemical approach. *Oikos* 88:119-128.
- von May, R., K. E. Reider, and K. Summers. 2009. Effect of body size on intraguild predation between tadpoles of bamboo-breeding poison frogs and predaceous mosquito larvae. *Journal of Freshwater Ecology* 24:431-435.
- Wagner, A., S. Hülsmann, H. Dörner, M. Janssen, U. Kahl, T. Mehner, and J. Benndorf. 2004. Initiation of the midsummer decline of *Daphnia* as related to predation, non-consumptive mortality and recruitment: a balance. *Archiv für Hydrobiologie* 160:1-23.
- Walls, S. C., and M. G. Williams. 2001. The effect of community composition on persistence of prey with their predators in an assemblage of pond-breeding amphibians. *Oecologia* 128:134-141.
- Walls, S. C., S. S. Belanger, and A. R. Blaustein. 1993. Morphological variation in a larval salamander: dietary induction of plasticity in head shape. *Oecologia* 96:162-168.

- Walston, L. J., and S. J. Mullin. 2008. Variation in amount of surrounding forest habitat influences the initial orientation of juvenile amphibians emigrating from breeding ponds. *Canadian Journal of Zoology* 86:141-146.
- Walston, L. J., and S. J. Mullin. 2007. Population responses of wood frog (*Rana sylvatica*) tadpoles to overwintered bullfrog (*Rana catesbeiana*) tadpoles. *Journal of Herpetology* 41:24-31.
- Ward, A., J. Liu, Z. Feng, and X. S. Xu. 2008. Light-sensitive neurons and channels mediate phototaxis in *C. elegans*. *Nature Neuroscience* 11:916-922.
- Werner, E. E. 1986. Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. *The American Naturalist* 128:319-341.
- Wheeler, C. A., N. E. Karraker, H. H. Welsh, and L. M. Ollivier. 2007. Diet of the Del Norte Salamander (*Plethodon elongatus*): differences by age, gender, and season. *Northwestern Naturalist* 88:85-94.
- Whiles, M. R., K. R. Lips, C. M. Pringle, S. S. Kilham, R. J. Bixby, R. Brenes, S. Connelley, J. C. Colon-Gaud, M. Hunt-Brown, A. D. Huryn, C. Montgomery, and S. Peterson. 2006. The effects of amphibian population declines on the structure and function of Neotropical stream ecosystems. *Frontiers in Ecology and the Environment* 4:27-34.
- Whiles, M. R., M. I. Gladyshev, N. N. Sushchik, O. N. Makhutova, G. S. Kalachova, S. D. Peterson, and K. J. Regester. 2010. Fatty acid analyses reveal high degrees of omnivory and dietary plasticity in pond-dwelling tadpoles. *Freshwater Biology* 55:1533-1547.
- Whiteman, H. H., J. P. Sheen, E. B. Johnson, A. VanDeusen, R. Cargille, and T. W. Sacco. 2003. Heterospecific prey and trophic polyphenism in larval tiger salamanders. *Copeia* 2003: 56-67.
- Wickramasinghe, D. D., K. L. Oseen, and R. J. Wassersug. 2007. Ontogenetic changes in diet and intestinal morphology in semi-terrestrial tadpoles of *Nannophrys ceylonensis* (Dicroglossidae). *Copeia* 2007:1012-1018.
- Wirsing, A. J., M. R. Heithaus, J. S. Brown, B. P. Kotler, and O. J. Schmitz. 2021. The context dependence of non-consumptive predator effects. *Ecology Letters* 24:113-129.
- 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. *Ecology* 91:549-559.

APPENDICES

Appendix A: Tables

Appendix A. Tables

Table 1. MANOVA and subsequent univariate ANOVAs for effects of cage treatment, habitat shading, and *Lithobates sylvaticus* tadpole body size on macroinvertebrate abundance by taxa. MANOVA results are reported on the same line where the independent variable is shown, whereas one-way ANOVA results are reported on the same line as the corresponding dependent variables. Bolded items indicate significant treatment effects, and “n,d” represents the numerator and denominator degrees of freedom.

Ind. & Dep. Variables	n,d	F	P
<u>Cage Treatment</u>	2,27	2.66	< 0.001
Anisoptera	2,27	2.60	0.080
Belostomatidae	2,27	1.00	0.372
Chaoboridae	2,27	0.75	0.475
Chironomidae	2,27	3.23	0.044
Corixidae	2,27	0.88	0.420
Culicidae	2,27	0.38	0.684
Dytiscidae	2,27	0.04	0.961
Gyrinidae	2,27	0.58	0.560
Haliplidae	2,27	2.00	0.141
Hydrophilidae adults	2,27	0.88	0.420
Nematoda	2,27	3.44	0.036
Notonectidae	2,27	0.75	0.475
Oligochaeta	2,27	0.80	0.452
Oligochaete Eggs	2,27	21.71	< 0.001
Physidae	2,27	1.92	0.152
Pleidae	2,27	1.08	0.344
Simuliidae	2,27	0.75	0.475
Trichoptera	2,27	23.59	< 0.001
Turbellaria	2,27	0.88	0.420
Zygoptera	2,27	0.75	0.475

Table 1. (continued).

Ind. & Dep. Variables	n,d	F	P
Total Abundance	2,27	2.56	0.083
<u>Shading Status</u>	1,90	8.78	< 0.001
Anisoptera	1,90	0.10	0.925
Belostomatidae	1,90	3.00	0.087
Chaoboridae	1,90	1.00	0.320
Chironomidae	1,90	1.89	0.173
Corixidae	1,90	2.00	0.161
Culicidae	1,90	3.04	0.084
Dytiscidae	1,90	0.39	0.536
Gyrinidae	1,90	0.33	0.565
Haliplidae	1,90	1.00	0.320
Hydrophilidae adults	1,90	2.00	0.161
Nematoda	1,90	39.24	< 0.001
Notonectidae	1,90	1.00	0.320
Oligochaeta	1,90	27.03	< 0.001
Oligochaete Eggs	1,90	15.95	< 0.001
Physidae	1,90	6.22	0.014
Pleidae	1,90	0.36	0.550
Simulidae	1,90	1.00	0.320
Trichoptera	1,90	9.31	0.003
Turbellaria	1,90	0.00	1.000
Zygoptera	1,90	1.00	0.320
Total Abundance	1,90	35.35	< 0.001
<u>Tadpole Size</u>	1,90	2.84	0.001
Anisoptera	1,90	0.13	0.718

Table 1. (continued).

Ind. & Dep. Variables	n,d	F	P
Belostomatidae	1,90	0.00	1.000
Chaoboridae	1,90	1.25	0.267
Chironomidae	1,90	2.23	0.139
Corixidae	1,90	0.63	0.431
Culicidae	1,90	2.28	0.135
Dytiscidae	1,90	1.28	0.260
Gyrinidae	1,90	0.42	0.520
Haliplidae	1,90	0.00	1.000
Hydrophilidae adults	1,90	0.63	0.431
Nematoda	1,90	17.69	< 0.001
Notonectidae	1,90	1.25	0.267
Oligochaeta	1,90	2.30	0.133
Oligochaete Eggs	1,90	5.01	0.028
Physidae	1,90	2.29	0.134
Pleidae	1,90	1.80	0.183
Simulidae	1,90	1.25	0.267
Trichoptera	1,90	6.77	0.011
Turbellaria	1,90	0.63	0.431
Zygoptera	1,90	1.25	0.267
Total Abundance	1,90	0.39	0.536
<u>Cage Treatment x Shade Status</u>	2,90	1.21	0.211
Anisoptera	2,90	2.08	0.131
Belostomatidae	2,90	1.00	0.372
Chaoboridae	2,90	0.75	0.475
Chironomidae	2,90	0.22	0.800
Corixidae	2,90	0.88	0.420

Table 1. (continued).

Ind. & Dep. Variables	n,d	F	P
Culicidae	2,90	1.77	0.176
Dytiscidae	2,90	0.26	0.774
Gyrinidae	2,90	0.25	0.779
Haliplidae	2,90	0.02	0.141
Hydrophilidae adults	2,90	0.88	0.420
Nematoda	2,90	0.59	0.557
Notonectidae	2,90	0.75	0.475
Oligochaeta	2,90	2.48	0.090
Oligochaete Eggs	2,90	2.61	0.079
Physidae	2,90	1.92	0.152
Pleidae	2,90	2.52	0.086
Simulidae	2,90	0.75	0.475
Trichoptera	2,90	5.41	0.006
Turbellaria	2,90	1.88	0.159
Zygoptera	2,90	0.75	0.475
Total Abundance	2,90	2.18	0.119
<u>Cage Treatment x Tadpole Size</u>	1,90	1.11	0.362
Anisoptera	1,90	1.69	0.197
Belostomatidae	1,90	0.00	1.000
Chaoboridae	1,90	1.25	0.267
Chironomidae	1,90	5.23	0.025
Corixidae	1,90	0.88	0.420
Culicidae	1,90	2.28	0.135
Dytiscidae	1,90	1.28	0.260
Gyrinidae	1,90	3.75	0.056
Haliplidae	1,90	0.00	1.000

Table 1. (continued).

Ind. & Dep. Variables	n,d	F	P
Hydrophilidae adults	1,90	0.63	0.431
Nematoda	1,90	0.16	0.690
Notonectidae	1,90	1.25	0.267
Oligochaeta	1,90	0.26	0.611
Oligochaete Eggs	1,90	0.47	0.497
Physidae	1,90	2.29	0.134
Pleidae	1,90	1.80	0.183
Simulidae	1,90	1.25	0.267
Trichoptera	1,90	3.02	0.087
Turbellaria	1,90	0.63	0.431
Zygoptera	1,90	1.25	0.267
Total Abundance	1,90	0.60	0.442
<u>Shading Status x Tadpole Size</u>	1,90	4.07	< 0.001
Anisoptera	1,90	0.88	0.351
Belostomatidae	1,90	0.00	1.000
Chaoboridae	1,90	1.25	0.267
Chironomidae	1,90	1.05	0.308
Corixidae	1,90	0.63	0.431
Culicidae	1,90	2.28	0.135
Dytiscidae	1,90	1.28	0.260
Gyrinidae	1,90	0.42	0.520
Haliplidae	1,90	0.00	1.000
Hydrophilidae adults	1,90	0.63	0.431
Nematoda	1,90	31.73	< 0.001
Notonectidae	1,90	1.25	0.267
Oligochaeta	1,90	1.98	0.163

Table 1. (continued).

Ind. & Dep. Variables	n,d	F	P
Oligochaete Eggs	1,90	0.00	1.000
Physidae	1,90	2.29	0.134
Pleidae	1,90	1.80	0.183
Simulidae	1,90	1.25	0.267
Trichoptera	1,90	3.02	0.087
Turbellaria	1,90	0.63	0.431
Zygoptera	1,90	1.25	0.267
Total Abundance	1,90	3.18	0.078
<u>Cage x Shade x Tadpole Size Treatment</u>	1,90	0.92	0.566
Anisoptera	1,90	0.09	0.764
Belostomatidae	1,90	0.00	1.000
Chaoboridae	1,90	1.25	0.267
Chironomidae	1,90	2.41	0.124
Corixidae	1,90	0.63	0.431
Culicidae	1,90	0.25	0.616
Dytiscidae	1,90	0.38	0.537
Gyrinidae	1,90	0.42	0.520
Haliplidae	1,90	0.00	1.000
Hydrophilidae adults	1,90	0.63	0.431
Nematoda	1,90	1.06	0.307
Notonectidae	1,90	1.25	0.267
Oligochaeta	1,90	0.10	0.752
Oligochaete Eggs	1,90	0.24	0.624
Physidae	1,90	2.29	0.134
Pleidae	1,90	1.80	0.183
Simulidae	1,90	1.25	0.267

Table 1. (continued).

Ind. & Dep. Variables	n,d	F	P
Trichoptera	1,90	6.77	0.011
Turbellaria	1,90	0.63	0.431
Zygoptera	1,90	1.25	0.267
Total Abundance	1,90	0.01	0.947

Table 2. MANOVA and subsequent one-way ANOVAs for effects of cage treatment, shading, and *Lithobates sylvaticus* tadpole body size on zooplankton abundance by taxa. MANOVA results are reported on the same line where the independent variable is shown, whereas one-way ANOVA results are reported on the same line as the corresponding dependent variables. Bolded items indicate significant treatment effects, and “n,d” represents the numerator and denominator degrees of freedom.

Ind. & Dep. Variables	n,d	F	P
<u>Cage Treatment</u>	2,27	5.05	< 0.001
Cladocera	2,27	4.52	0.013
Copepoda Adults	2,27	2.44	0.093
Copepoda Nauplii	2,27	13.13	< 0.001
Ostracoda	2,27	6.80	0.002
Total Abundance	2,27	14.91	< 0.001
<u>Shading Status</u>	1,90	15.33	< 0.001
Cladocera	1,90	16.36	< 0.001
Copepoda Adults	1,90	6.86	0.010
Copepoda Nauplii	1,90	0.17	0.683
Ostracoda	1,90	50.79	< 0.001
Total Abundance	1,90	16.12	< 0.001
<u>Tadpole Size</u>	1,90	4.10	0.004
Cladocera	1,90	13.26	< 0.001
Copepoda Adults	1,90	4.31	0.041
Copepoda Nauplii	1,90	1.13	0.290
Ostracoda	1,90	4.59	0.035
Total Abundance	1,90	7.13	0.009
<u>Cage Treatment x Shade Status</u>	2,90	3.65	0.001
Cladocera	2,90	2.80	0.066

Table 2. (continued).

Ind. & Dep. Variables	n,d	F	P
Copepoda Adults	2,90	0.40	0.670
Copepoda Nauplii	2,90	7.29	0.001
Ostracoda	2,90	2.29	0.107
Total Abundance	2,90	5.62	0.005
<u>Cage Treatment x Tadpole Size</u>	1,90	1.85	0.126
Cladocera	1,90	1.00	0.321
Copepoda Adults	1,90	0.83	0.365
Copepoda Nauplii	1,90	0.31	0.577
Ostracoda	1,90	2.63	0.108
Total Abundance	1,90	0.39	0.534
<u>Shade Status x Tadpole Size</u>	1,90	5.52	0.001
Cladocera	1,90	2.14	0.150
Copepoda Adults	1,90	0.01	0.916
Copepoda Nauplii	1,90	19.67	< 0.001
Ostracoda	1,90	2.92	0.091
Total Abundance	1,90	10.74	0.001
<u>Cage x Shade x Tadpole Size Treatment</u>	1,90	1.25	0.297
Cladocera	1,90	0.28	0.600
Copepoda Adults	1,90	1.31	0.256
Copepoda Nauplii	1,90	1.82	0.181
Ostracoda	1,90	0.91	0.343
Total Abundance	1,90	0.02	0.877

Table 3. MANOVA and subsequent one-way ANOVAs for effects of cage treatment, habitat shading, and *Lithobates sylvaticus* tadpole body size on relative fluorescence (RFU), % dissolved oxygen, temperature (°C), and biofilm mass (mg). MANOVA results are reported on the same line where the independent variable is shown, whereas one-way ANOVA results are reported on the same line as the corresponding dependent variables. Bolded items indicate significant treatment effects, and “n,d” represents the numerator and denominator degrees of freedom.

Ind. & Dep. Variables	n,d	F	P
<u>Cage Treatment</u>	2,27	5.40	< 0.001
Relative Fluorescence	2,27	0.90	0.410
Dissolved Oxygen	2,27	0.83	0.441
Temperature	2,27	11.72	< 0.001
Biofilm Mass	2,27	5.62	0.005
<u>Shading Status</u>	1,90	125.43	< 0.001
Relative Fluorescence	1,90	15.60	< 0.001
Dissolved Oxygen	1,90	205.75	< 0.001
Temperature	1,90	321.05	< 0.001
Biofilm Mass	1,90	0.13	0.719
<u>Tadpole Size</u>	1,90	7.42	< 0.001
Relative Fluorescence	1,90	9.13	0.003
Dissolved Oxygen	1,90	6.74	0.011
Temperature	1,90	1.43	0.235
Biofilm Mass	1,90	8.82	0.004
<u>Cage Treatment x Shade Status</u>	2,90	5.68	< 0.001
Relative Fluorescence	2,90	1.34	0.267
Dissolved Oxygen	2,90	9.84	< 0.001
Temperature	2,90	11.80	< 0.001

Table 3. (continued).

Ind. & Dep. Variables	n,d	F	P
Biofilm Mass	2,90	0.92	0.403
<u>Cage Treatment x Tadpole Size</u>	1,90	3.49	0.010
Relative Fluorescence	1,90	4.78	0.031
Dissolved Oxygen	1,90	8.34	0.005
Temperature	1,90	0.14	0.709
Biofilm Mass	1,90	1.02	0.316
<u>Shade Status x Tadpole Size</u>	1,90	1.68	0.163
Relative Fluorescence	1,90	1.45	0.232
Dissolved Oxygen	1,90	0.71	0.401
Temperature	1,90	4.20	0.043
Biofilm Mass	1,90	0.72	0.398
<u>Cage x Shade x Tadpole Size Treatment</u>	1,90	0.72	0.584
Relative Fluorescence	1,90	0.01	0.939
Dissolved Oxygen	1,90	2.67	0.106
Temperature	1,90	0.48	0.490
Biofilm Mass	1,90	0.05	0.818

Table 4. MANOVA and subsequent one-way ANOVAs for effects of cage treatment, habitat shading, and *Lithobates sylvaticus* tadpole size class on % tadpole survival per mesocosm and growth (mm/day). MANOVA results are reported in the row where the independent variable is listed, whereas one-way ANOVA results are reported on the line that corresponds to each dependent variable. Bolded items indicate significant treatment effects, and “n,d” represents the numerator and denominator degrees of freedom. Degrees of freedom are lower than for previous analyses because these analyses were restricted to mesocosms containing tadpoles, whereas previous analyses included controls.

Ind. & Dep. Variables	n,d	F	P
<u>Cage Treatment</u>	1,18	1.83	0.150
% Survival	1,18	3.50	0.065
Growth in Length	1,18	0.84	0.363
Growth in Width	1,18	1.12	0.292
<u>Shading Status</u>	1,72	27.84	< 0.001
% Survival	1,72	0.02	0.887
Growth in Length	1,72	64.80	< 0.001
Growth in Width	1,72	73.64	< 0.001
<u>Tadpole Size</u>	1,72	28.99	< 0.001
% Survival	1,72	37.92	< 0.001
Growth in Length	1,72	4.05	0.048
Growth in Width	1,72	45.11	< 0.001
<u>Cage Treatment x Shade Status</u>	1,72	8.23	< 0.001
% Survival	1,72	2.60	0.111
Growth in Length	1,72	2.40	0.125
Growth in Width	1,72	5.07	0.027

Table 4. (continued).

Ind. & Dep. Variables	n,d	F	P
<u>Cage Treatment x Tadpole Size</u>	1,72	10.44	< 0.001
% Survival	1,72	0.32	0.574
Growth in Length	1,72	28.01	< 0.001
Growth in Width	1,72	6.85	0.011
<u>Shade Status x Tadpole Size</u>	1,72	0.55	0.652
% Survival	1,72	1.59	0.211
Growth in Length	1,72	< 0.01	0.963
Growth in Width	1,72	< 0.01	0.986
<u>Cage x Shade x Tadpole Size Treatment</u>	1,72	2.88	0.042
% Survival	1,72	3.12	0.081
Growth in Length	1,72	0.15	0.701
Growth in Width	1,72	2.13	0.149

Table 5. One-way ANOVAs for effects of cage treatment and habitat shading on final body lengths and head widths (mm) of *Lithobates sylvaticus* tadpoles, blocked by mesocosm. Bolded items indicate significant treatment effects, and “n,d” represents the numerator and denominator degrees of freedom.

Ind. & Dep. Variables	n,d	F	P
<u>Cage Treatment</u>			
Body Length	1,18	0.58	0.448
Head Width	1,18	0.60	0.442
<u>Shading Status</u>			
Body Length	1,72	26.96	< 0.001
Head Width	1,72	55.98	< 0.001
<u>Cage x Shade</u>			
Body Length	1,72	2.15	0.147
Head Width	1,72	0.12	0.735

Appendix B: Figures

Appendix B: Figures

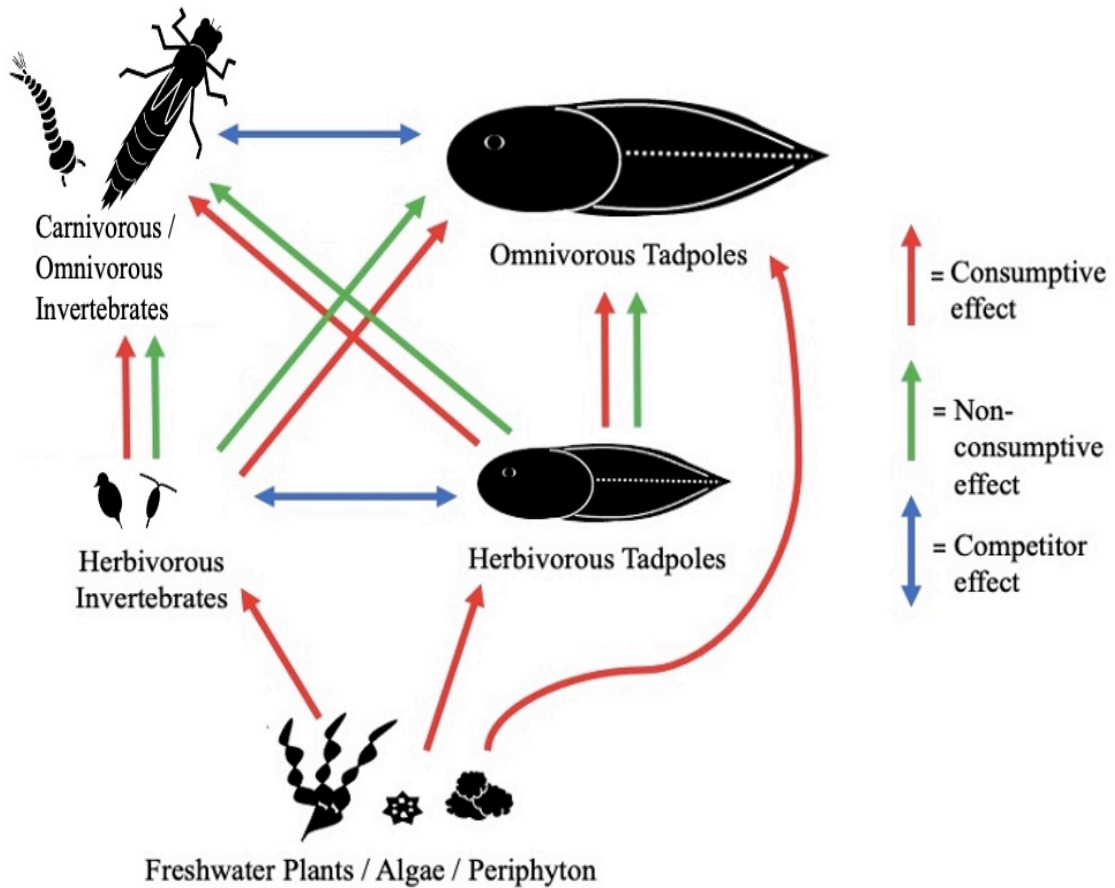


Figure 1. Food web illustrating trophic relationships within and among tadpoles and invertebrates. Omnivorous tadpoles and carnivorous invertebrates exert competitive effects on each other, as well as consumptive and non-consumptive predatory effects on herbivorous tadpoles and invertebrates, whereas herbivorous tadpoles and invertebrates exert competitive effects on each other.

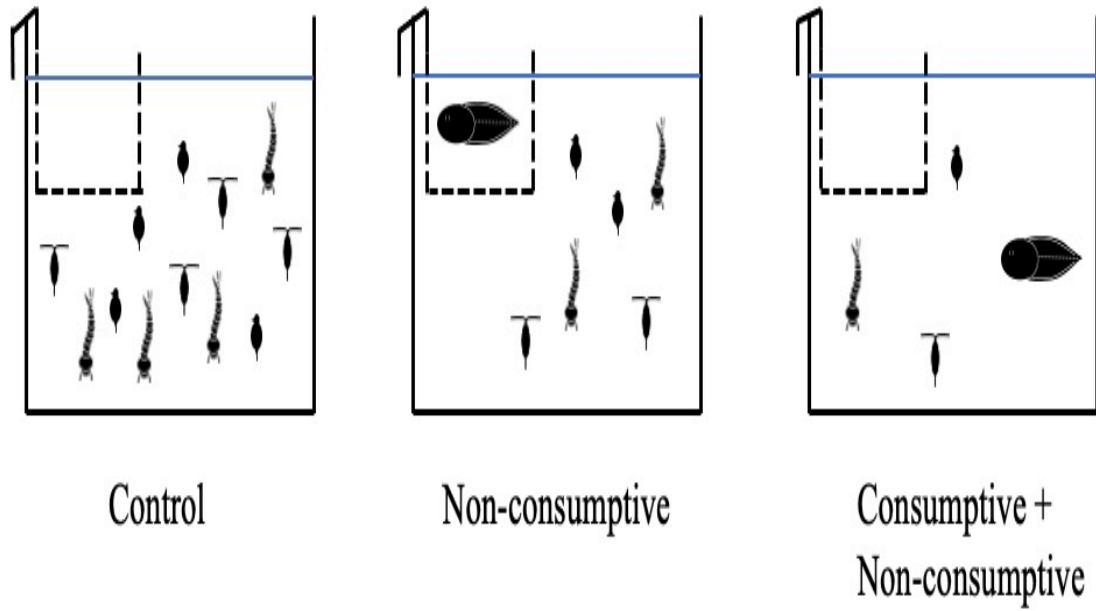


Figure 2. Hypothesized differences in macroinvertebrate and zooplankton abundance by treatment. Abundance was expected to be highest in control mesocosms lacking *Lithobates sylvaticus* tadpoles, intermediate in caged-tadpole mesocosms, and lowest in mesocosms with free-swimming tadpoles.

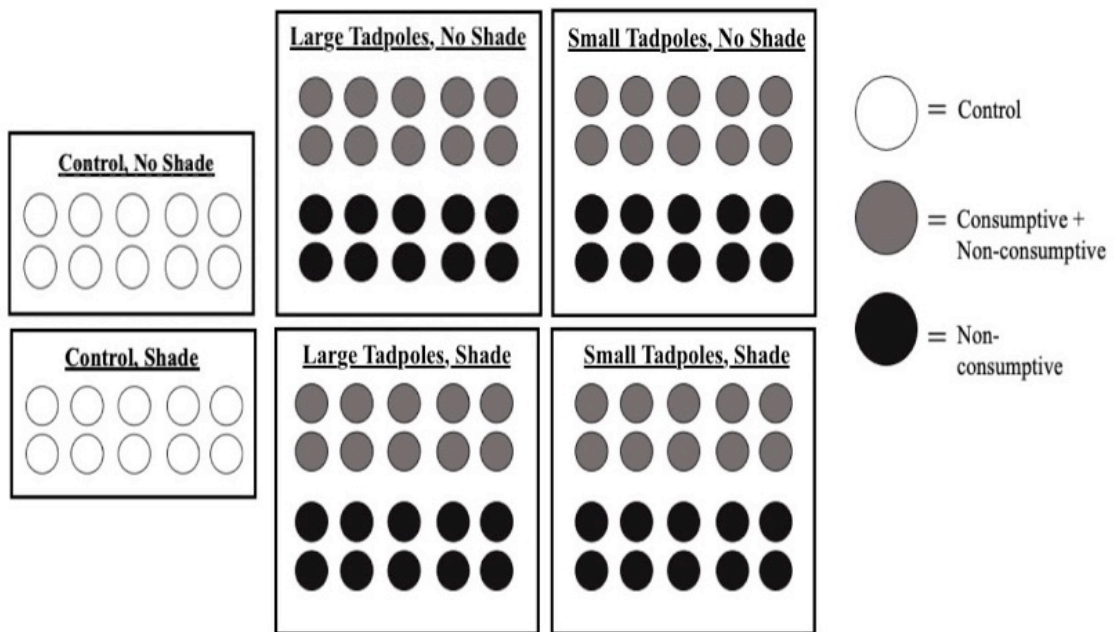


Figure 3. Mesocosm layout / organization by treatment group (shade and *Lithobates sylvaticus* tadpole size) and subgroup (control, consumptive + non-consumptive, and non-consumptive). Each circle represents one mesocosm, with ten mesocosms per subgroup.

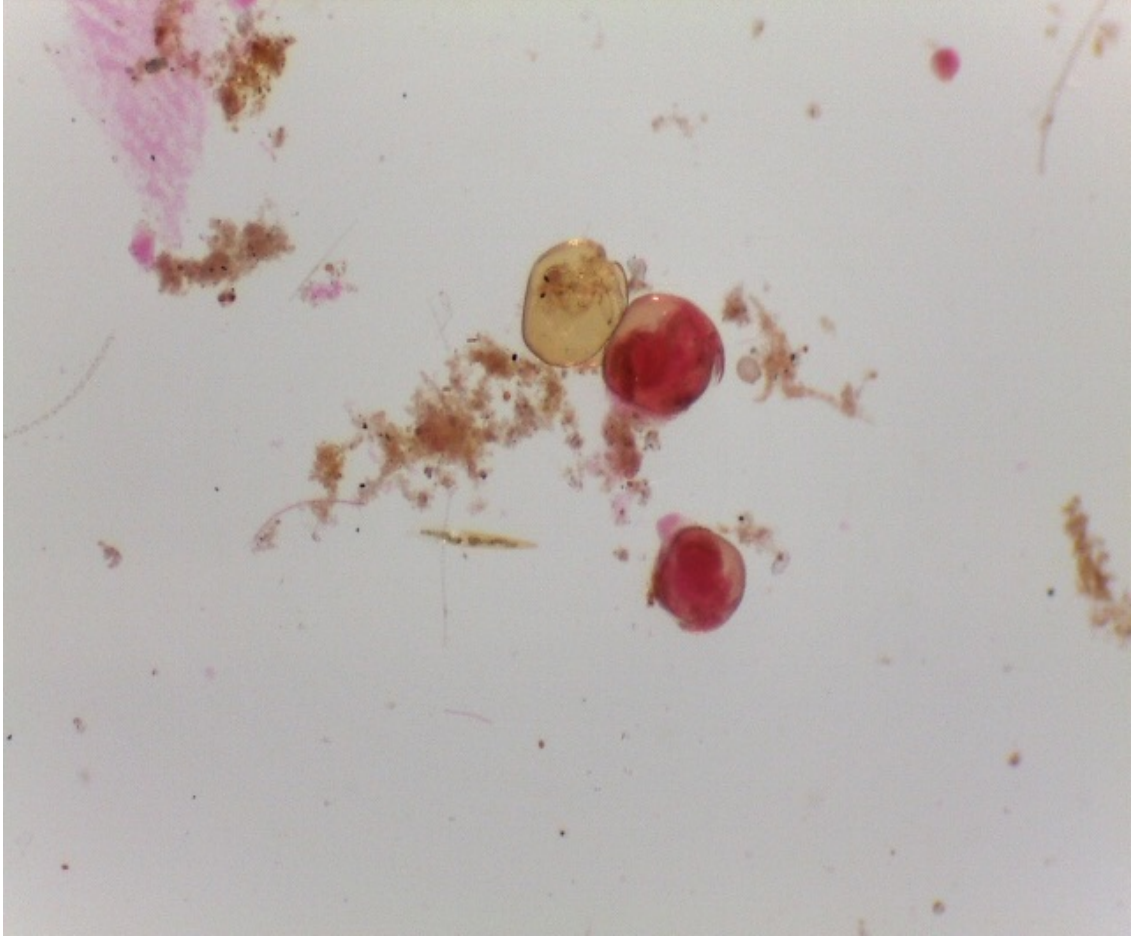


Figure 4. Three cladocerans found in small intestine contents of a *Lithobates sylvaticus* tadpole from the Cumberland Ranger District of Daniel Boone National Forest, preserved in 10% buffered formalin and stained with Rose Bengal (35x dissection microscopy).



Figure 5. A chironomid found in the small intestine contents of a *Lithobates sylvaticus* tadpole from the Cumberland Ranger District of Daniel Boone National Forest preserved in 10% buffered formalin and stained with Rose Bengal (35x dissection microscopy).

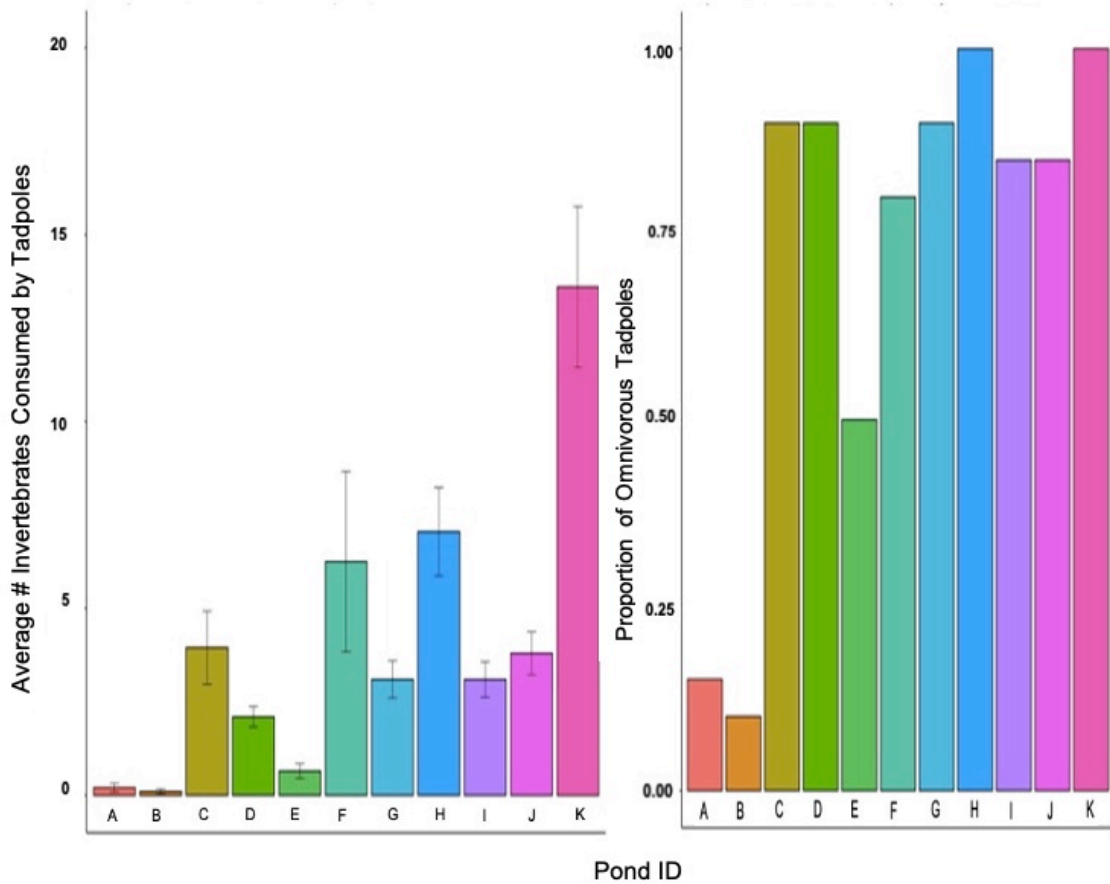


Figure 6. Average number of invertebrates consumed by *Lithobates sylvaticus* tadpoles (left) and proportions of omnivorous tadpoles (right) across 11 ponds (increasing estimated pond surface area from left to right) in the Cumberland Ranger District of the Daniel Boone National Forest; estimates based on contents of the first 10 mm of the small intestines.

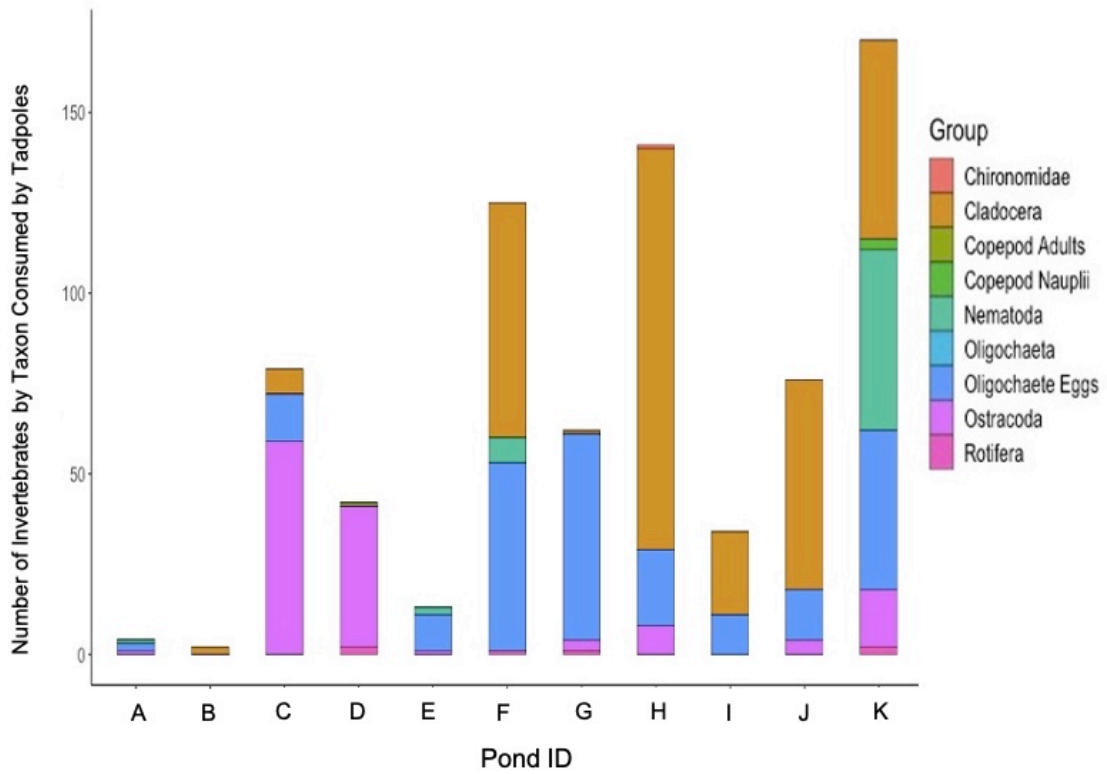


Figure 7. Total number of invertebrates per taxon consumed by *Lithobates sylvaticus* tadpoles across 11 ponds in the Cumberland Ranger District of the Daniel Boone National Forest (increasing estimated pond surface area from left to right).

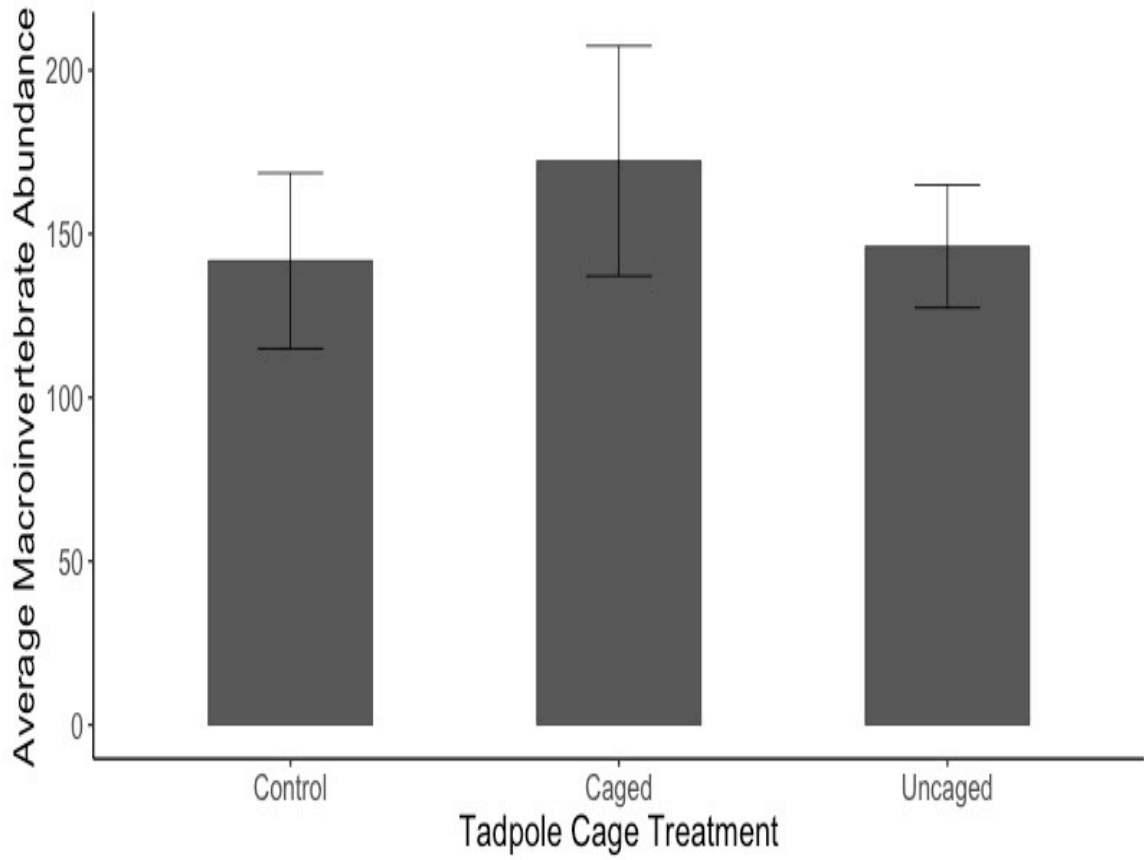


Figure 8. Average abundance (± 1 S.E.) of macroinvertebrates in mesocosms by *Lithobates sylvaticus* tadpole cage treatment.

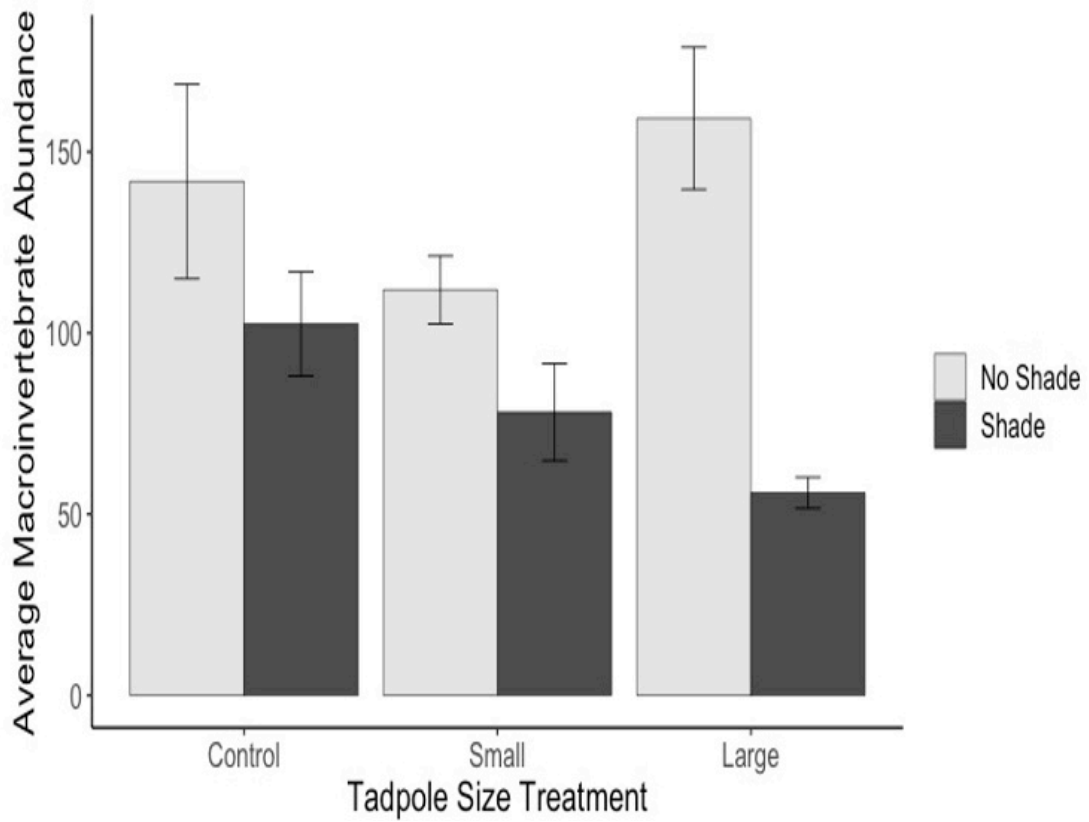


Figure 9. Average abundance (± 1 S.E.) of macroinvertebrates in mesocosms by *Lithobates sylvaticus* tadpole body size and habitat shading treatments.

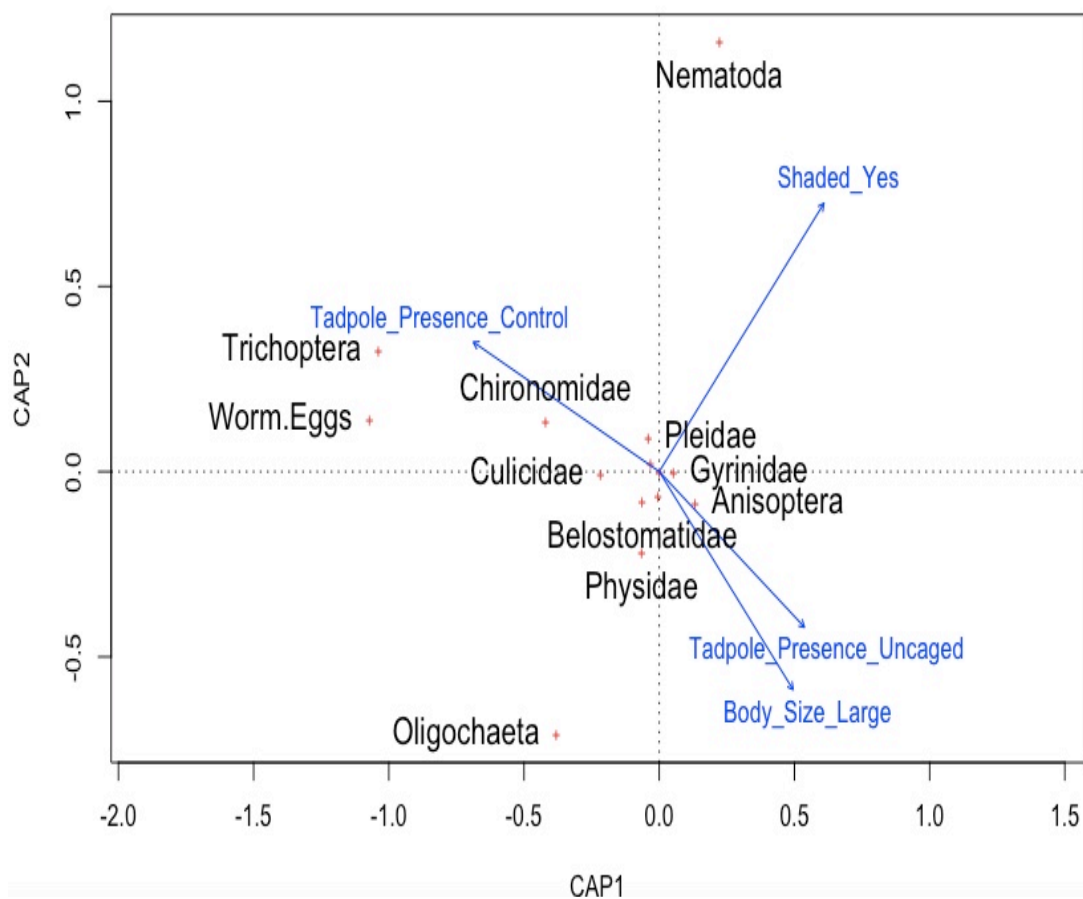


Figure 10. Distance-based redundancy capscale ordination of macroinvertebrate abundance by taxon based on *Lithobates sylvaticus* tadpole presence, tadpole size, and degree of habitat shading. Each labelled red plus represents the relative abundance of each macroinvertebrate group in relation to the independent variables shown in blue. The distance measure used for the ordination was Bray-Curtis.

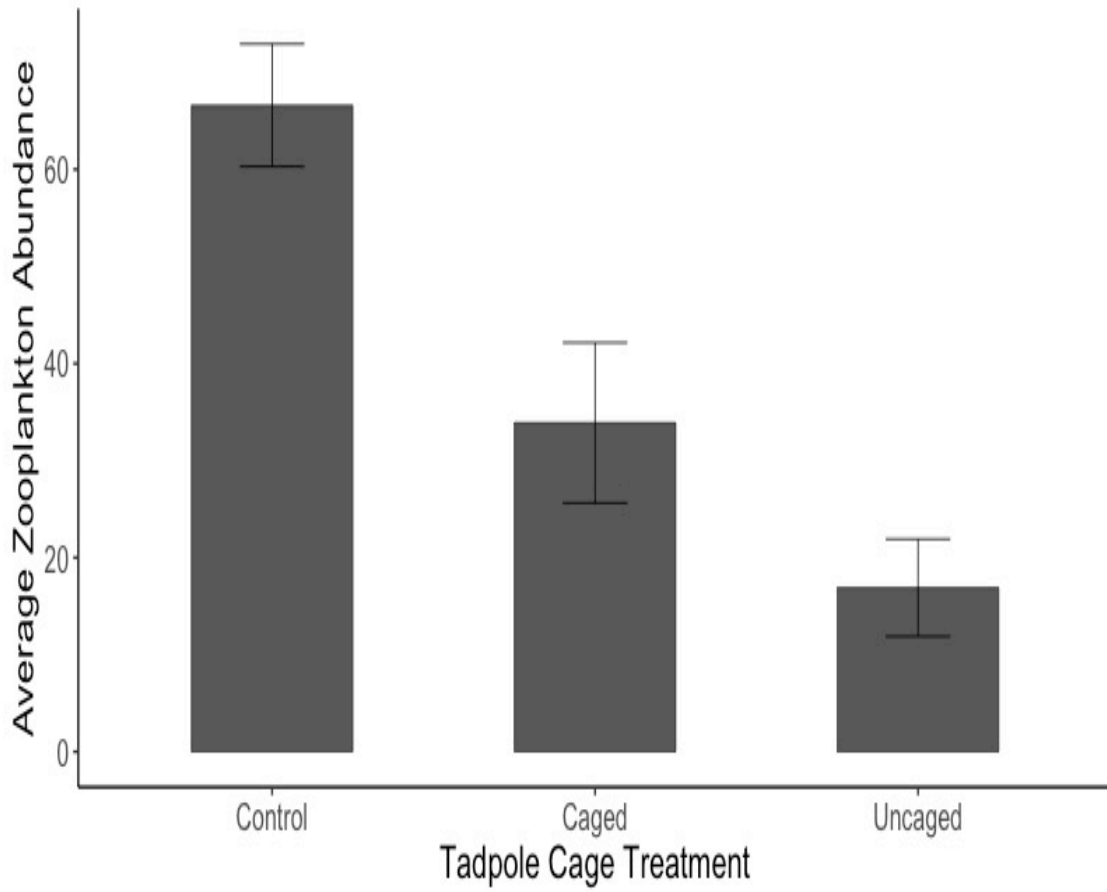


Figure 11. Average zooplankton (± 1 S.E.) abundance in mesocosms by *Lithobates sylvaticus* tadpole cage treatment.

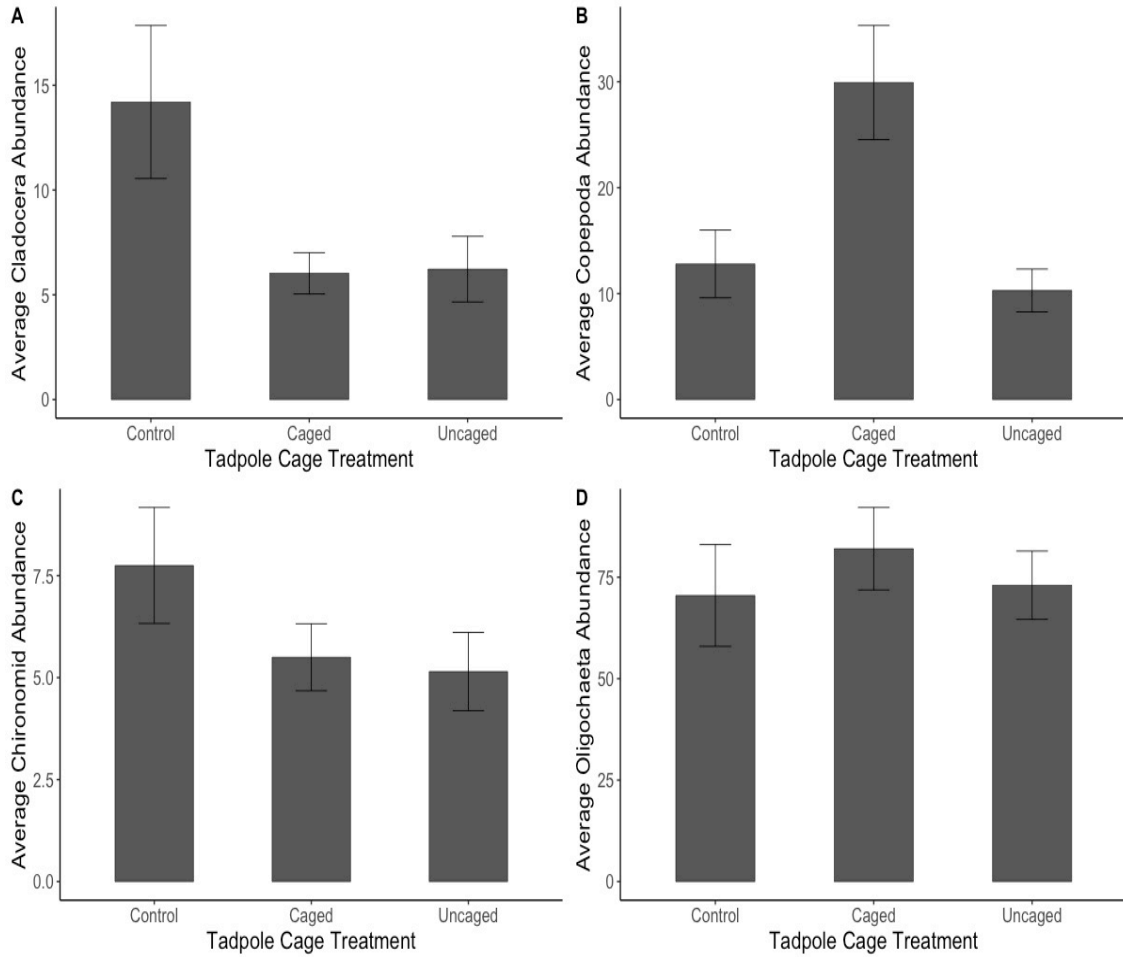


Figure 12. Average abundances (± 1 S.E.) of two common zooplankton (A. Cladocera, B. Copepoda) and macroinvertebrate (C. Chironomidae, D. Oligochaeta) taxa in mesocosms by *Lithobates sylvaticus* tadpole cage treatment.

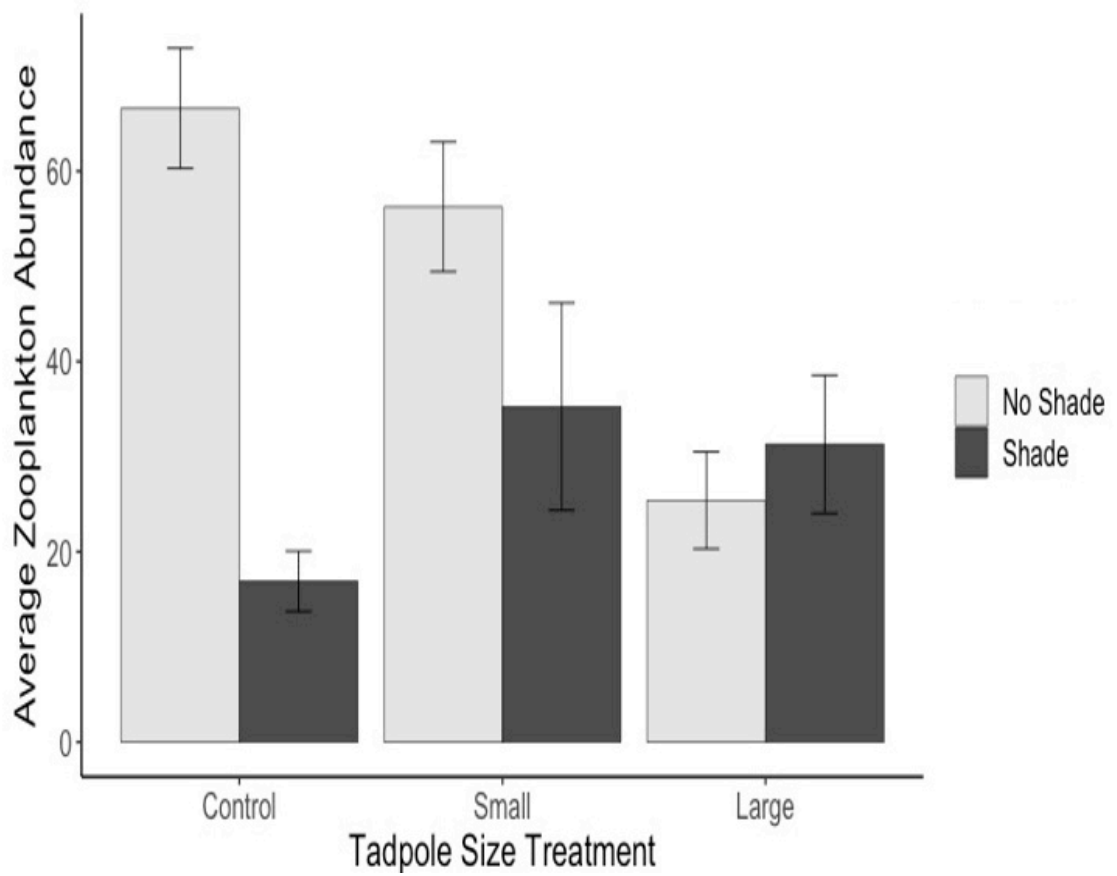


Figure 13. Average abundance (± 1 S.E.) of zooplankton in mesocosms by *Lithobates sylvaticus* tadpole body size and habitat shading treatments.

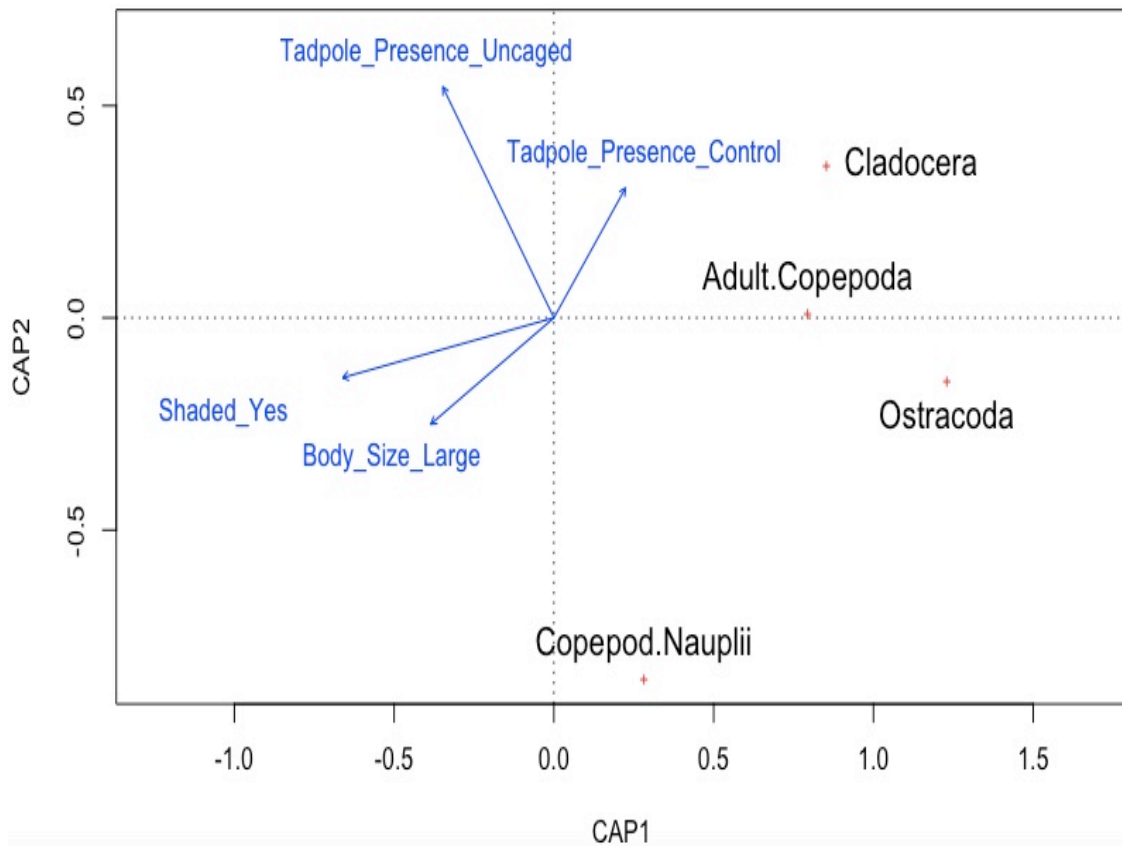


Figure 14. Distance-based redundancy capscale ordination of zooplankton abundance by taxon based on *Lithobates sylvaticus* tadpole presence, tadpole size, and degree of habitat shading. Each labelled red plus sign represents the relative abundance of each zooplankton group in relation to the independent variables shown in blue. The distance measure used for the ordination was Bray-Curtis.

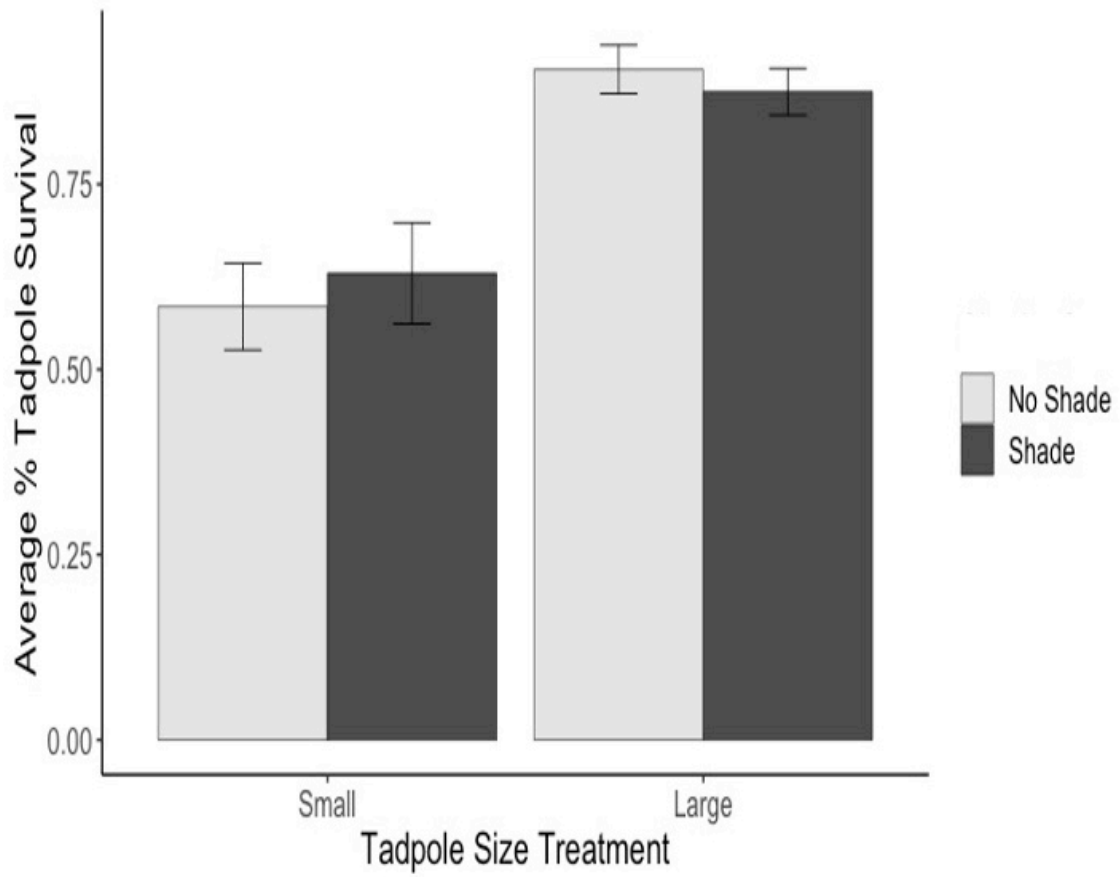


Figure 15. Average % survival (± 1 S.E.) of *Lithobates sylvaticus* tadpoles in mesocosms by tadpole body size and habitat shading treatments.

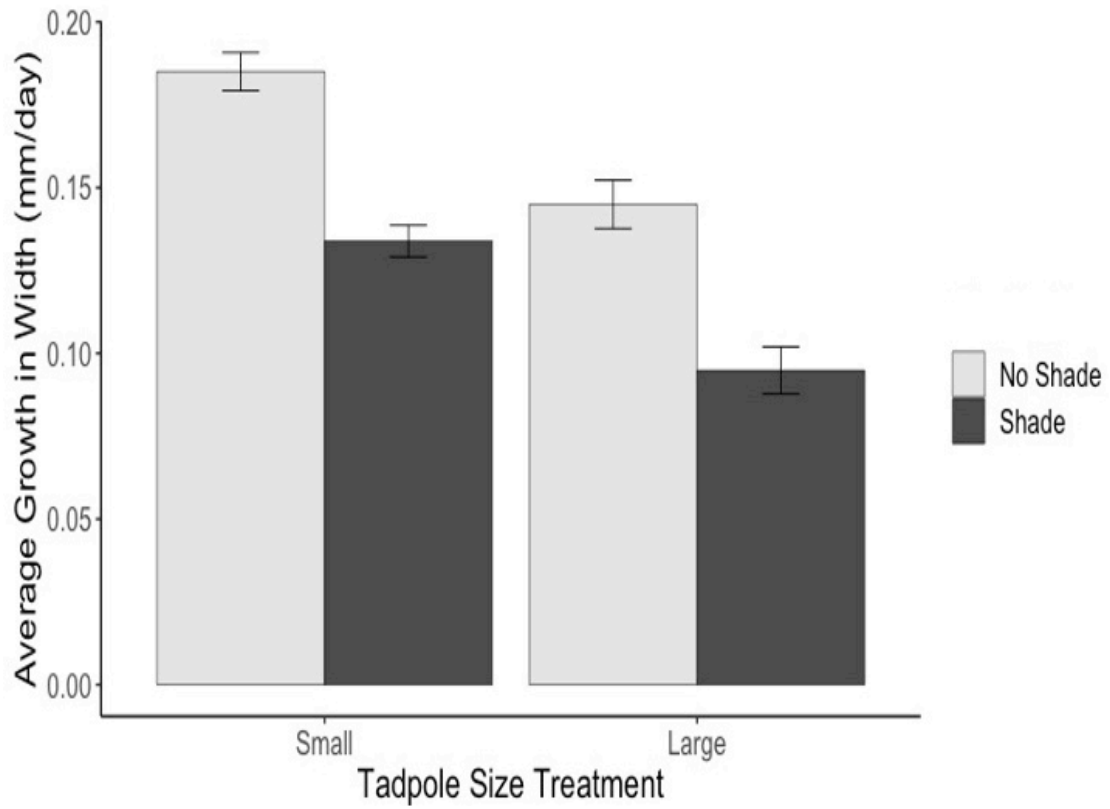


Figure 16. Average growth in head width (mm/day; ± 1 S.E.) of *Lithobates sylvaticus* tadpoles in mesocosms by tadpole body size and habitat shading treatments.

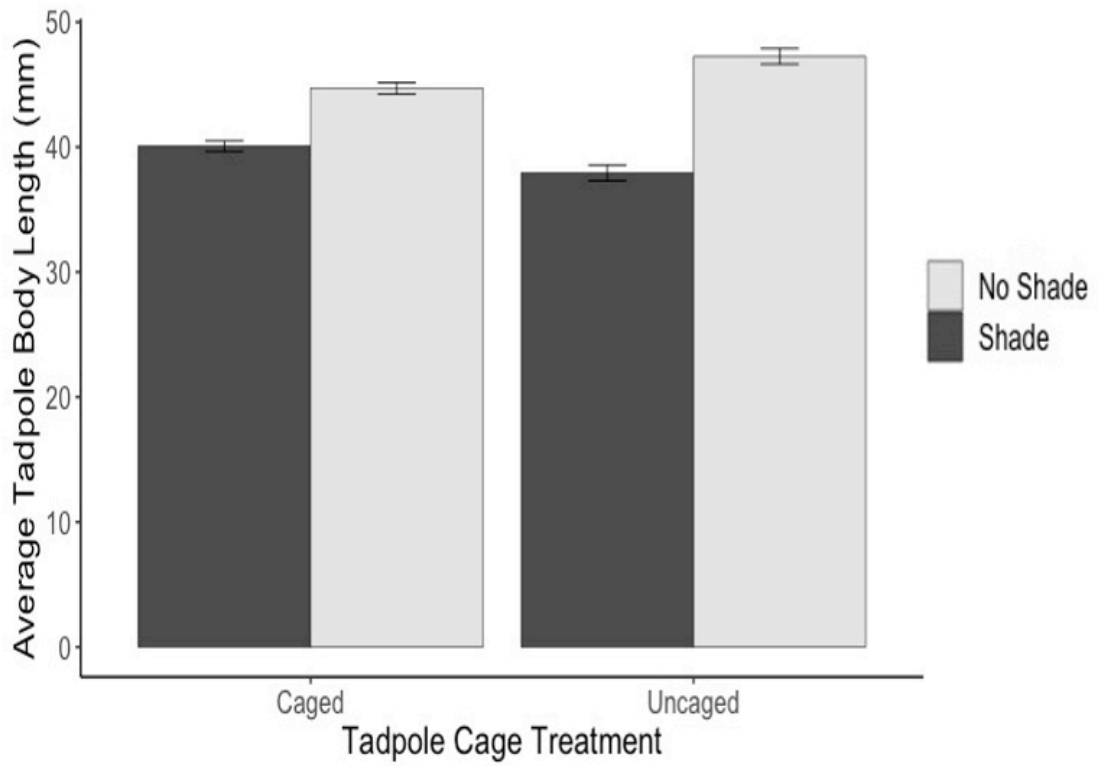


Figure 17. Average body length (mm; ± 1 S.E.) of *Lithobates sylvaticus* tadpoles in mesocosms by tadpole cage and habitat shading treatments.