Selective Predation by Pond-Breeding Salamanders in Ephemeral Wetlands of Ohio and Illinois

Brock P. Struecker,[1,2] Joseph R. Milanovich,[1] Mollie McIntosh,[3] Martin B. Berg,[1] and Matthew E. Hopton[4,5]

[1]*Department of Biology, Loyola University Chicago, Chicago, Illinois, USA*
[3]*Department of Biology, Xavier University, Cincinnati, Ohio, USA*
[4]*United States Environmental Protection Agency, Office of Research and Development, Center for Environmental Solutions and Emergency Response, Water Infrastructure Division, Stormwater Management Branch, Cincinnati, Ohio, USA*

ABSTRACT.—Larval amphibians are important components of ephemeral wetland ecosystems, where they are abundant and perform important ecological functions. Larval pond-breeding salamanders (genus *Ambystoma*) are the primary vertebrate predators in fishless, ephemeral wetland systems, where they consume large amounts of aquatic invertebrate prey. However, the mechanisms in which larval salamanders affect aquatic communities are poorly understood. We compared stomach contents of larval pond-breeding salamanders from two regions in the midwestern United States to assess their diets for evidence of prey selection. We found larval salamanders exhibited selective predation for certain taxa and functional feeding groups. Our results provide a possible mechanism in which larval pond-breeding salamanders affect aquatic invertebrate communities and shape ephemeral wetland ecosystem processes.

Amphibians are key consumers that comprise a primary component of wetland ecosystems. Amphibians can occur in high densities in ephemeral wetlands and are a large constituent of wetland biodiversity, especially in their larval stage (Lannoo, 2005; Gibbons et al., 2006). Therefore, amphibian larvae have significant ecological impacts within these systems through a variety of processes (Hocking and Babbitt, 2014). For example, larval amphibians cycle nutrients in aquatic systems that provide available nutrients for other aquatic organisms (Seale, 1980; Seale and Beckvar, 1980; Whiles et al., 2013) and provide pathways for energy transfer between aquatic and terrestrial ecosystems (Regester et al., 2008; Earl et al., 2014; Schriever et al., 2014; Capps et al., 2015). Larval amphibians also influence aquatic communities through competition and consumption (Walls, 1995; Ranvestel et al., 2004; Benoy, 2008). Multiple studies have found larval pond-breeding salamanders to have both direct and indirect effects on food webs within their respective ecosystems, and studies suggest these organisms may be keystone species in lentic aquatic habitats (Holomuzki et al., 1994; reviewed in Davic and Welsh, 2004; Benoy, 2008; Regester et al., 2008). Yet, a deeper understanding about how larval salamander predation shapes wetland communities is largely unknown. Thus, examining how amphibian larvae predate aquatic invertebrate (i.e., macroinvertebrates and zooplankton) communities could shed light on how larval predatory amphibians shape aquatic communities.

Predatory pond-breeding salamanders (genus *Ambystoma*) are abundant in many fishless ephemeral wetlands in the midwestern United States (Lannoo, 2005), where densities of larvae can vary widely depending on species and wetland characteristics (Werner et al., 2007). For example, Van Buskirk and Smith (1991) reported densities of *Ambystoma laterale* (Blue-spotted Salamanders) ranging from <20 larvae/m^2 to 158 larvae/m^2 on Isle Royale in Lake Superior, Michigan, USA. In addition to occurring in potentially high densities within ephemeral wetlands, predatory salamander larvae can consume large numbers of invertebrates throughout their development (Whiles et al., 2004; DuRant and Hopkins, 2008; Chaparro-Herrera et al.,

2011). The abundance of larval pond-breeding salamanders and the high volume of prey they consume suggest these salamanders could significantly alter the abundance of prey in ephemeral wetlands.

Aquatic amphibian predation on zooplankton and macroinvertebrates (hereafter aquatic invertebrates) has been found to significantly alter the demography of aquatic invertebrate communities as well as influence prey behavior (Dodson, 1974; Morin, 1981; Holomuzki et al., 1994; Wissinger et al., 1999). Yet the mechanisms for how amphibians shape aquatic invertebrate communities through predation are ill-defined. Specifically, it is unknown if larval salamanders affect aquatic invertebrate communities by disproportionately consuming certain prey (i.e., selective predation). Selective predation by larval salamanders could be the mechanism by which they alter the demography of aquatic invertebrate communities, similar to the effect selective predation by eastern newts (*Notophthalmus viridescens*) had on amphibian communities as evidenced by Morin (1981). If selective predation by larval pond-breeding salamanders occurs, considering the ecological function (i.e., functional feeding groups) of their prey could also provide a mechanism for the larger, indirect effects observed by others (e.g., Holomuzki et al., 1994). Other research has shown disproportionate predation by salamanders on functional feeding groups of aquatic invertebrates in Appalachian streams (Keitzer and Goforth, 2013). Therefore, an investigation of prey selection and selection of functional feeding groups by larval pond-breeding salamanders is warranted.

Here we investigate the diet composition of larval pond-breeding salamanders (hereafter salamanders) and community composition (i.e., density, functional feeding groups, richness) of aquatic invertebrates across a series of ephemeral wetlands in northeast Illinois and southwest Ohio. We tested whether the composition of larval salamander stomach contents differed significantly from the community composition of wetland water columns.

MATERIALS AND METHODS

Study Species.—We investigated three species of salamanders across two sampling locations in the midwestern United States;

[2]Corresponding Author. E-mail: brock.struecker@gmail.com
[5]Corresponding Author. E-mail: hopton.matthew@epa.gov

TABLE 1. Location of wetlands, average wetland surface area (size, m²), number of days each wetland held water within study period (DWW), and densities of larval salamander species. Bold values indicate wetlands having water the entire sampling period.

Wetland	State	Size (m²)	DWW (days)	Salamander density ± SD (animals/m²)		
				A. jeffersonianum	A. tigrinum	A. laterale
Ethel's West	Illinois	376.74	59			2.62 ± 1.59
Ethel's East	Illinois	942.82	97		0.42 ± 0.47	0.35 ± 0.52
Ethel's Center	Illinois	1,538.38	114		0.08 ± 0.15	0.04 ± 0.06
Grainger	Illinois	803.62	85		0.03 ± 0.04	0.22 ± 0.25
Rollins Savanna	Illinois	741.96	171		1.28 ± 0.90	0.02 ± 0.06
Farbach Werner	Ohio	21.32	27	0.75 ± 0.96		
Woodland Mound	Ohio	457.14	**118**	29.00 ± 46.88		
Spring Pond	Ohio	1,509.59	**118**	1.67 ± 3.56		
Oak Glen	Ohio	199.61	**118**	3.67 ± 8.20		
Glenwood Gardens	Ohio	3,749.14	56	0.57 ± 1.13		
Shawnee Forest	Ohio	34.37	**118**	30.62 ± 33.22		

Ambystoma tigrinum tigrinum (Eastern Tiger Salamanders) and *Ambystoma laterale* (Blue-spotted Salamanders) in Illinois, and *Ambystoma jeffersonianum* (Jefferson's Salamanders) in Ohio—the most abundant species present in our sampling. *Ambystoma tigrinum* is the largest bodied of the three species, typically grows to nearly 20 cm as an adult, breeds in a variety of water bodies from permanent to ephemeral, and occurs throughout the eastern United States from Florida to Minnesota and from the Mississippi River Valley east to the Atlantic Coast (Lannoo, 2005). *Ambystoma laterale* and *A. jeffersonianum* have similar life histories and ecologies and are known to hybridize where sympatric (Lannoo, 2005). These species are smaller than *A. tigrinum* and reach 14–18 cm as adults. *Ambystoma laterale* and *A. jeffersonianum* are distributed from southern Canada south to Kentucky and Virginia and east to Maine, with *A. laterale* representing the northern half and *A. jeffersonianum* representing the southern half of that distribution, with an area of hybridization in the middle (Lannoo, 2005:fig. 1).

Illinois Sampling Design.—We sampled five wetlands in Lake County, Illinois for larval salamanders and water column invertebrates 13 May to 3 September 2015 (Table 1). Wetlands ranged in size from 376 m² to 1,538 m² and were surrounded by a matrix of forest, agriculture, and urbanization. All wetlands were fishless; however, each wetland contained at least one species of larval anuran (Bullfrogs; *Lithobates catesbeiana*, Green Frogs; *Lithobates clamitans*, and Chorus Frogs; *Pseudacris triseriata*) and one or both species of salamanders, *A. tigrinum* or *A. laterale*.

Illinois Larval Amphibian Sampling.—We quantitatively sampled amphibians biweekly during the study period. Each sampling period consisted of 1) three consecutive nights of trapping using 15 to 25 Promar minnow traps (46 × 25 cm) with trapping density dictated by wetland area, and 2) "pipe sampling" at the time of each visit using methods proposed by Werner et al. (2007), where a 52 × 27-cm galvanized steel cylinder was used to sample a 0.2-m² area of the sediments and associated water column. Pipe samples were chosen by selecting locations evenly distributed throughout the wetland each sampling period. Samples were taken by carefully approaching the wetland and then quickly pushing the cylinder into the substratum. Nets (23 × 15 cm) were employed to remove all animals within the cylinder with circular sweeps until 10 consecutive empty sweeps were taken (Mullins et al., 2004). We took five pipe samples per wetland; however, if the wetland area was reduced because of drying, and samples could not be taken at least 2 m apart, the number of samples was reduced accordingly. Similarly if, because of drying, a wetland area did not allow for 25 minnow traps

spaced evenly at a minimum of 2 m apart, trap density was reduced to 15 to maintain spacing. Density of larval salamanders and nonpredatory amphibians (i.e., anuran larvae) were quantified by assuming that one minnow trap (Ousterhout et al., 2015) and/or five pipe samples sampled approximately 1 m² of wetland.

For diet analysis, once per month we collected five to 10 larval *A. tigrinum* (50 total) and *A. laterale* (47 total) across all wetlands. Specimens were sacrificed using an Orajel® solution (Cecala et al., 2007) immediately after capture and were fixed within 5 min of sacrifice, using 10% neutral buffer formalin for 24 h, and stored in 70% EtOH (ethyl alcohol). Specimens were later measured (snout–vent length [SVL], anterior portion of the snout to the posterior portion of the vent; 0.1 mm), weighed (wet mass; ±0.01 g), and dissected to remove the stomach and intestinal tracts. Stomach and intestinal tracts were preserved in 70% EtOH and contents were identified to the lowest possible taxon using Merritt et al. (2008) and Thorp and Covich (2001).

Illinois Invertebrate Sampling.—Water column invertebrates were sampled with 80-μm Wisconsin plankton nets (20-cm diameter, 37-cm length). Plankton nets were attached to a 1.5-m wooden handle and swept within a 1-m² area to sample water column invertebrates at three randomly selected replicate locations within each wetland once per month. Five total plankton net sweeps per replicate were taken in the water column. Invertebrate samples were preserved in 70% EtOH. Each replicate sample was subsampled to process samples more efficiently. Water column invertebrates were sampled on the same day larval salamanders were sacrificed. All organisms were identified to family, and genus when possible, using Merritt et al. (2008) and Thorp and Covich (2001).

Ohio Sampling Design.—We sampled six wetlands located in Hamilton, Butler, and Clermont Counties, Ohio from 29 March to 24 July 2012. Wetlands ranged in size from 21 m² to 3,749 m² (Table 1). This region contains several ephemeral and permanent wetlands and is surrounded by a matrix of urban, agriculture, and forested land. All wetlands were fishless and contained larval *A. jeffersonianum*. Each wetland contained one to several species of larval anurans including *Anaxyrus americanus* (American Toads), *Acris crepitans* (Northern Cricket Frogs), *Hyla chrysoscelis* (Cope's Gray Treefrogs), *L. catesbeiana*, *L. clamitans*, and *P. crucifer* (Spring Peepers).

Ohio Larval Amphibian Sampling.—Amphibians were quantitatively sampled using the "pipe sampling" technique (Werner et al., 2007) as described above. Five to 10 pipe samples were taken per wetland, depending upon wetland size. Five samples were
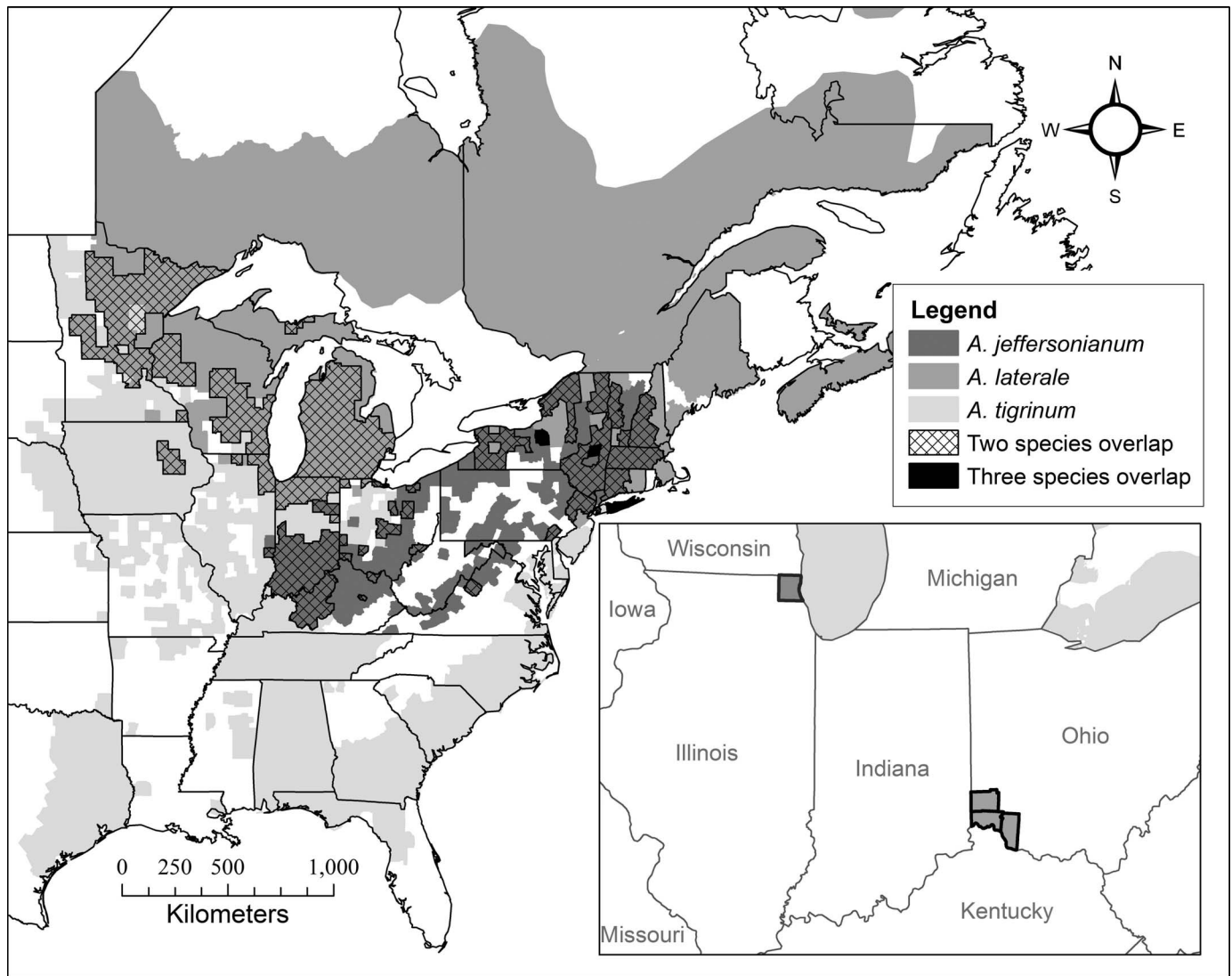
Fɪɢ. 1. Range maps of *A. jeffersonianum*, *A. laterale*, and *A. tigrinum* (IUCN, 2014; Lannoo, 2005). Zoomed detail shows highlighted counties where study sites were located in northeast Illinois and southwest Ohio.

collected from wetlands <300 m² and 10 samples were collected from wetlands ≥300m². Samples were randomly located at least 2 m from adjacent samples. If the wetland area was reduced because of drying, and samples could not be taken at least 2 m apart, the number of samples was reduced accordingly. Density (number of individuals/m²) was calculated as the number of individuals captured within five pipe samples (0.2 m² each). For diet analysis, we collected a series of larval *A. jeffersonianum* from six wetlands (*n* = 20 to 30 per wetland; 325 total). Within 30 min of collection, all salamanders were euthanized by immersion in a 0.1% solution of neutral pH-buffered MS-222 (ethyl m-amino-benzoate methanesulfonate; Gentz, 2007). Samples were then processed as above and stomach contents were identified to the lowest taxon possible.

Ohio Invertebrate Sampling.—Water column invertebrates were sampled using a dipper consisting of a plastic container (11-cm diameter; 350-mL volume) that sampled the upper water column and surface. The number of samples collected was standardized based on site size. For example, 15 (for wetlands <300 m²) or 30 dips (wetlands ≥300 m²) were taken at each wetland. All dipper samples from within a wetland were combined and rinsed through a 63-µm sieve and preserved in 70% EtOH. These

semiquantitative dip samples included mainly small macroin-vertebrates and vegetation, if present. Dipper samples were taken on the same days as larval salamanders were sacrificed. In the laboratory all organisms were sorted and identified to family level using Merritt et al. (2008) and Thorp and Covich (2001).

Statistical Analyses.—We used nonmetric multidimensional scaling (NMDS) ordinations using Bray-Curtis dissimilarities to identify if diet items of salamanders were consumed in different relative proportions to water column invertebrate communities within wetlands. We used analysis of similarities (ANOSIM) post hoc tests to identify significant dissimilarities between diet items and water column invertebrates. We further investigated differences in salamander diets and available water column invertebrates with Ivlev's Electivity Index to determine selective predation of salamanders on certain taxa and functional feeding groups. This index uses relative abundances of diet items and water column invertebrates, where positive electivity values indicate taxa low in relative abundance in the water column, yet high in diets, suggesting preferred selection of those taxa, whereas negative electivity values indicate taxa with high relative abundance in the water column, yet low in diets, suggesting avoidance of those taxa. All percentage data (including relative
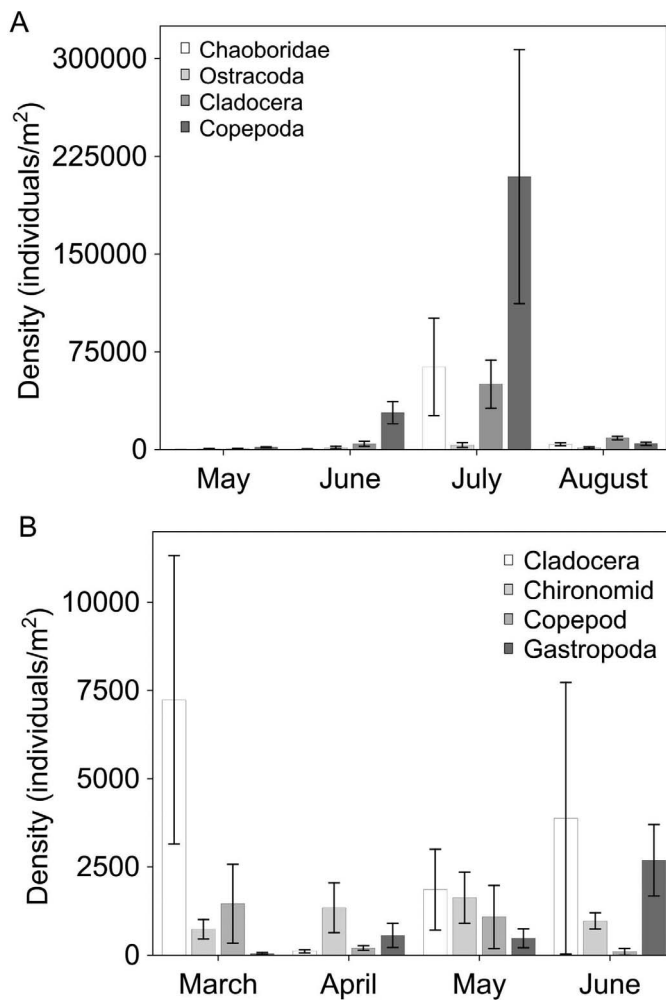
FIG. 2. Monthly densities of the four most abundant aquatic invertebrate taxa found in water columns in (A) Illinois and (B) Ohio wetlands.
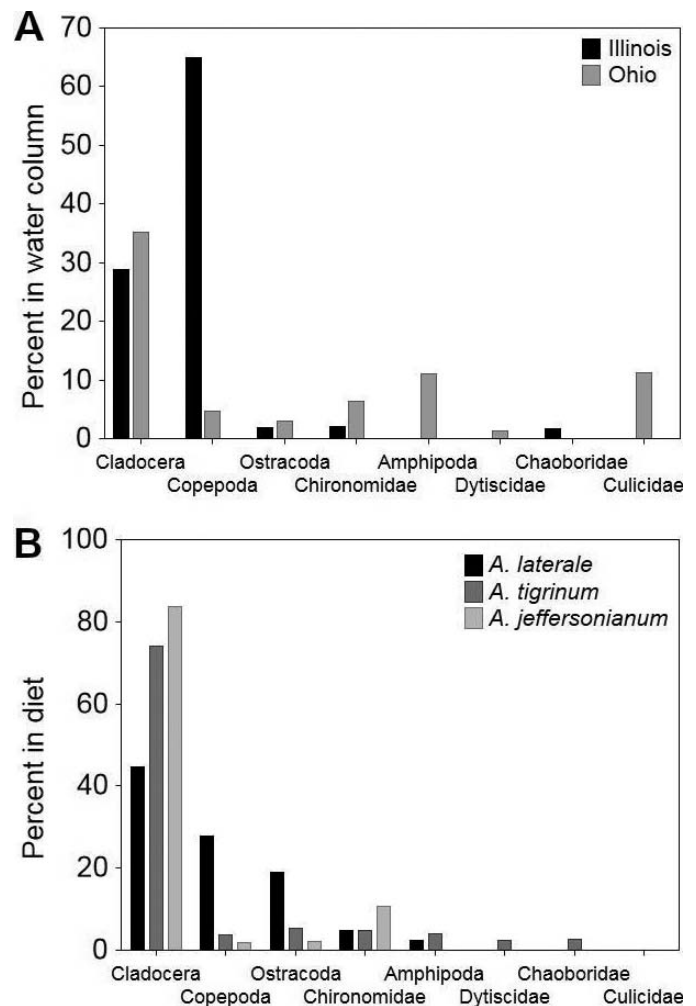

FIG. 3. Percentage (relative abundance) of the most abundant aquatic invertebrate taxa in both (a) water column samples and (b) stomachs of salamanders. Water column aquatic invertebrate taxa are categorized by location and diet items are categorized by salamander species where *A. laterale* and *A. tigrinum* were found only in Illinois and *A. jeffersonianum* only in Ohio wetlands.

abundances) were square-root transformed. All analyses were performed in Statistica 12.0 (Statsoft, Inc., Tulsa, Oklahoma) with the exception of NMDS and ANOSIM, which were performed in PRIMER 6 (PRIMER-E Ltd., Plymouth).

RESULTS

Wetlands in both Illinois and Ohio differed in surface area and days with water across our sampling months (Table 1). All wetlands in Illinois dried completely by the end of the study period and four wetlands in Ohio never dried (Table 1). Densities of salamanders differed across wetlands with higher densities in Ohio wetlands compared to Illinois (Table 1).

Illinois Wetlands.—We collected 1,072 *A. tigrinum* and 814 *A. laterale* in Illinois wetlands during the study. Mean (±standard deviation [SD]) densities were 0.5 (±0.7) *A. tigrinum*/m^2 and ranged from 0 to 5.3/m^2 and 0.3 (±0.5) *A. laterale*/m^2, with a range of 0 to 2.88/m^2 across all wetlands (Table 1). Other larval amphibian densities ranged from 0 to 1.5/m^2. We identified 28,009 individual invertebrates from the water column representing 42 taxa across Illinois wetlands. Invertebrate communities were dominated by Cladocera (*Daphnia*), Copepoda, and Diptera (*Chaoborus*; Fig. 2A; Appendix 1). A total of 4,829 invertebrates representing 30 taxa were found in stomachs of salamander larvae in Illinois wetlands (Fig. 3B; Appendix 1). Diets of both

species of salamander consisted mostly of Cladocera, Copepoda, Ostracoda, Chironomidae, Amphipoda, and smaller numbers of other macroinvertebrates (Fig. 3B). *Ambystoma tigrinum* and *A. laterale* consumed different relative proportions of prey. For example, *A. laterale* diets consisted of 41% Cladocera, 27% Copepoda, and 19% Ostracoda, whereas *A. tigrinum* consumed 74% Cladocera, with the next highest taxon group being Ostracoda, comprising only 5% of diets (Fig. 3B). Per capita consumption was estimated to be 24.78 invertebrates/day (average number of individual taxa found in each stomach) by *A. laterale* and 104.29 invertebrates/day by *A. tigrinum*.

Ohio Wetlands.—We collected 554 *A. jeffersonianum* during the study. Larval *A. jeffersonianum* density averaged 6.7 (±21.2)/m^2 across all wetlands, with the highest densities found in March. Larval anuran density averaged 25.1 (±55.45)/m^2 across all wetlands. In total, we quantified 21,776 invertebrates representing 48 taxa across Ohio wetlands (Fig. 2A; Appendix 2). Water column invertebrate communities were dominated by Cladocera followed by Gastropoda, Copepoda, and Diptera larvae (Chaoboridae, Culcidae, and Chironomidae; Fig. 3A; Appendix 2). Diets of *A. jeffersonianum* were dominated by Cladocera (83%) and Chironomidae (10%), with much smaller proportions of
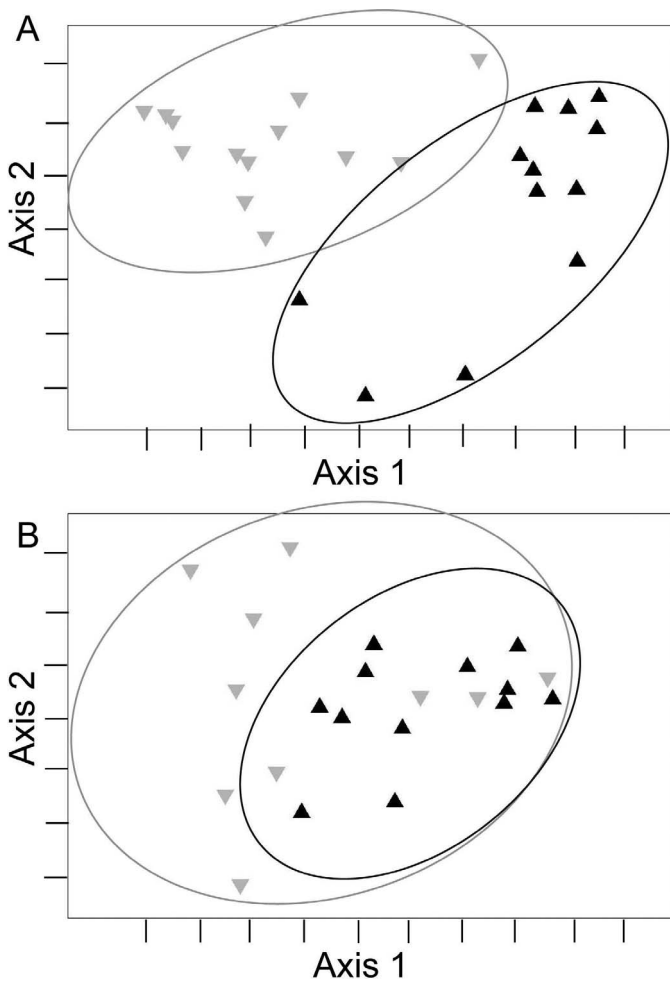
FIG. 4. NMDS ordinations of the relative abundance of salamander diet items (e.g., stomach content, SC; black) and water column (WC, gray) aquatic invertebrate taxa for (a) Illinois and (b) Ohio. Each point represents a sampling month at an individual wetland.

FIG. 5. Mean Ivlev's Electivity Index scores with ± standard error (SE) bars for (a) water column taxa and (b) invertebrate functional feeding groups. Positive values indicate salamanders selecting for invertebrate taxa/functional feeding groups, whereas negative values represent selection against invertebrate taxa/functional feeding groups.

other taxa such as Copepoda and Ostracoda (Fig. 3B; Appendix 3). A total of 15,882 invertebrates representing 25 taxa were consumed by *A. jeffersonianum* throughout our sampling period and per capita consumption was, on average, 47.32 invertebrates/day.

Diet Analyses.—NMDS ordination showed diet items in larval salamanders were distinct from water column aquatic invertebrate taxa (Fig. 4) in which diet items and water column invertebrate relative abundances were dissimilar in Illinois ($P <$ 0.001, Global R = 0.626) and Ohio ($P =$ 0.022, Global R = 0.159). Thus, the taxa larval salamanders consumed were distinctly different than what was available to them in the water column. Although salamander selectivity for water column invertebrates differed among species, there were a few similarities (Fig. 5). All salamander species had positive electivity values for Cladocera and Chironomidae (Diptera) and had negative electivity values for Copepoda. Copepods had high relative abundances in the water column but low relative abundances in salamander diets, whereas Cladocera and Chironomidae (more so for Chironomidae) had relatively low abundances in the water column but were represented in much higher relative abundances in diets. All *Ambystoma* species had positive electivity values for collector–filterers and collector–gatherers, and negative electivity values for predators (Fig. 5).
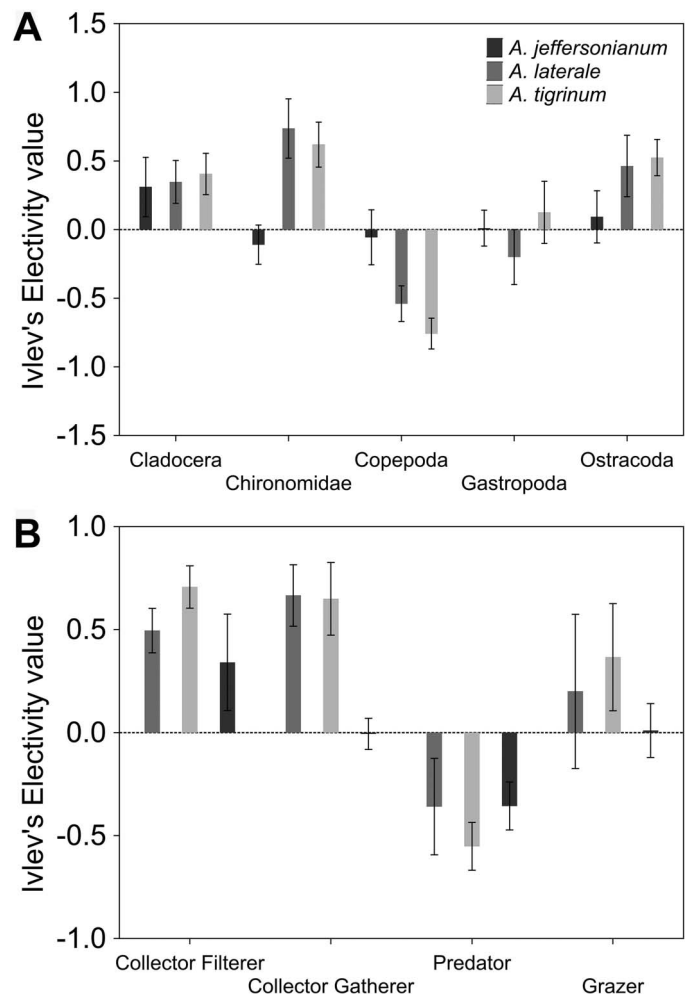
DISCUSSION

We provide evidence that pond-breeding salamander larvae feed selectively from the water column, with a disproportionately high amount of cladocerans and a disproportionately low amount of copepods in salamander diets (Fig. 4). These results are consistent with other studies that have shown cladocerans as a major component of larval salamander diets (Holomuzki et al., 1994, Whiles et al., 2004, Bardwell et al., 2007). For example, Whiles et al. (2004) found *Ambystoma cingulatum* diets dominated by Cladocera in South Carolina and Florida wetlands. Selection for cladocerans over copepods has been shown in other planktivores such as fish (Fink et al., 2012) as well as in other pond-breeding salamander species (Ghioca-Robrecht and Smith, 2008). This may be a function of the ability of copepods to evade predation compared to other, more slow-moving prey such as cladocerans (Amundsen et al., 2009; Peterka and Matena, 2009), making cladoceran prey items more easily captured by larval salamanders. Other research suggests selection for prey items may be related to the predator's perception of prey size. For example, O'Brien et al. (1976) suggested predators' perceived overall size of prey based on the size of their prey's eye spot. This may partly explain the selection for cladocerans and against copepods in our study, as

Daphnia species (the most abundant cladocerans in our study wetlands) have large eye spots whereas many copepods have small or no eye spots. Larval salamanders may also select cladocerans such as *Daphnia* for their high nutritional value compared to the lower nutritional value of copepods (Andersen and Hessen, 1991). The ability to select more-nutritious prey has been exhibited by fish, but evidence salamanders exhibit this behavior is limited (Reissig et al., 2015).

Larval salamanders selected for Chironomidae, which represented a relatively low percentage of diet items but some of the highest electivity values. Yet, larval forms of chironomids in this study region generally inhabit benthic habitats rather than open water columns. Chironomidae occur in high abundance and are an important diet item for other aquatic taxa (i.e., fish; Anderson et al., 2012) and may be important to salamander species across a wide variety of aquatic habitats and geographic locations because they are one of the most ubiquitous taxonomic groups of aquatic insects (Merritt et al., 2008). Chironomids are a common constituent in the diets of pond-breeding salamanders, as observed in other studies (Holomuzki et al., 1994; Benoy et al., 2002; Whiles et al., 2004). Regester et al. (2008) found Chironomidae to be a significant contributor to larval production of pond-breeding salamanders, but it is not known if salamanders readily identify prey that is more nutritious. The disparity between the abundance of chironomid larvae in water column samples and salamander stomachs could be the result of salamanders feeding in benthic habitats in addition to the water column. However, the majority of the remaining taxa found as salamander prey, except Amphipoda, are typical water column inhabitants. Therefore, it is difficult to determine whether chironomid larvae entered the water column and then were readily eaten by salamanders, or if salamanders sought prey associated with wetland sediments. In shallow, depressional wetlands, the distance between the water column and benthic habitats is likely a short transition, which may allow either salamanders or aquatic invertebrates to readily move from one to the other. Additionally, chironomid larvae were found in water column samples, suggesting that some did move from the bottom of wetlands into the water column.

Larval salamanders selected against predatory invertebrates while selecting for all other functional feeding groups, which may have consequences for ecosystem processes. The variation in selectivity of particular functional feeding groups may partly explain the observations by Holomuzki et al. (1994) that salamander larvae (genus *Ambystoma*) had no significant effect on invertebrate densities directly, but had a significant impact on primary production of wetlands. A similar effect has been observed when comparing aquatic systems with and without vertebrate predators (e.g., Herbst et al., 2009). Selection against predators may be shifting the proportion of functional feeding groups in these systems, effectively enhancing the number of predators and thereby increasing primary production through a trophic cascade. This cascading effect was observed by Herbst et al. (2009) when comparing trout stream to fishless stream communities. Indirect effects of selective predation have been observed in other studies as well (Turner and Mittelbach, 1990). However, it is difficult to attribute any one variable or species to ecological processes within dynamic food web systems, as their interactions are complex and interwoven. This was not the initial objective of our study and, therefore, our data collection is poorly aimed at determining if trophic cascading is occurring as a result of larval salamander selective predation. Our data indicate selective predation exists and provide a basis for further investigation into the effects this may have on whole ecosystem processes within ephemeral wetlands.

Further understanding of how larval salamanders may shape ephemeral wetland food webs may underscore their importance across the landscape and increase conservation efforts. This would be especially useful in the midwestern United States, where habitat loss and fragmentation have contributed to the decline of salamander populations. Therefore, we suggest that further investigation of ephemeral wetland food webs and the impact of larval salamanders within ephemeral wetlands are needed. We also suggest that including functional feeding groups in further research may provide interesting avenues for investigation. For example, altered ratios in wetland functional feeding groups may unveil indirect effects of salamander predation. Studies centered on larval salamander selection of functional feeding groups, branching from the research we present here, may provide insight into the full ecological significance of larval predatory pond-breeding salamanders in isolated wetlands.

Literature Cited

Amundsen, P. A., A. Siwertsson, R. Primicerio, and T. Bøhn. 2009. Long-term responses of zooplankton to invasion by a planktivorous fish in a subarctic watercourse. Freshwater Biology 54:24–34.

Andersen, T., and D. O. Hessen. 1991. Carbon, nitrogen, and phosphorus content of freshwater zooplankton. Limnology and Oceanography 36:807–814.

Anderson, T. J., R. S. Stelzer, H. G. Drecktrah, and S. L. Eggert. 2012. Secondary production of Chironomidae in a large eutrophic lake: implications for lake sturgeon production. Freshwater Science 31:365–378.

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

Benoy, G. A. 2008. Tiger salamanders in prairie potholes: a "fish in amphibian's garments?". BioOne Wetland 28:464–472.

Benoy, G. A., T. D. Nudds, and E. Dunlop. 2002. Patterns of habitat and invertebrate diet overlap between tiger salamanders and ducks in prairie potholes. Hydrobiologia 481:47–59.

Capps, K. A., K. A. Berven, and S. D. Tiegs. 2015. Modelling nutrient transport and transformation by pool-breeding amphibians in forested landscapes using a 21-year dataset. Freshwater Biology 60:500–511.

Cecala, K. K., S. J. Price, and M. E. Dorcas. 2007. A comparison of the effectiveness of recommended doses of MS-222 (tricaine methanesulfonate) and Oragel® (benzocaine) for amphibian anesthesia. Herpetological Review 38:63–66.

CHAPARRO-HERRERA, D. D., S. NANDINI, S. S. S. SARMA, AND L. ZAMBRANO. 2011. Feeding behaviour of larval *Ambystoma mexicanum*. Amphibia-Reptilia 32:509–517.

DAVIC, R. D., AND H. H. WELSH JR. 2004. On the ecological roles of salamanders. Annual Review of Ecology, Evolution, and Systematics 35:405–434.

DODSON, S. I. 1974. Zooplankton competition and predation: an experimental test of the size–efficiency hypothesis. Ecology 553:605–613.

DURANT, S. E., AND W. A. HOPKINS. 2008. Amphibian predation on larval mosquitoes. Canadian Journal of Zoology 86:1159–1164.

EARL, J. E., P. O. COSTELLO, K. E. COHAGEN, AND R. D. SEMLITSCH. 2014. Effects of subsidy quality on reciprocal subsidies: how leaf litter species changes frog biomass export. Oecologia 175:209–218.

FINK, P., A. KOTTSIEPER, M. HEYNEN, AND J. BORCHERDING. 2012. Selective zooplanktivory of an invasive Ponto-Caspian mysid and possible consequences for the zooplankton community structure of invaded habitats. Aquatic Sciences 74:191–202.

GENTZ, E. J. 2007. Medicine and surgery of amphibians. Ilar Journal 48:255–259.

GHIOCA-ROBRECHT, D. M., AND L. M. SMITH. 2008. Feeding ecology of polymorphic larval barred tiger salamanders in playas of the Southern Great Plains. Canadian Journal of Zoology-Revue Canadienne De Zoologie 86:554–563.

GIBBONS, J. W., C. T. WINNE, D. E. SCOTT, J. D. WILLSON, X. GLAUDAS, K. M. ANDREWS, B. D. TODD, L. A. FEDEWA, L. WILKINSON, R. N. TSALIAGOS, ET AL. 2006. Remarkable amphibian biomass and abundance in an isolated wetland: implications for wetland conservation. Conservation Biology 20:1457–1465.

HERBST, D. B., E. L. SILLDORFF, AND S. D. COOPER. 2009. The influence of introduced trout on the benthic communities of paired headwater streams in the Sierra Nevada of California. Freshwater Biology 54:1324–1342.

HOCKING, D. J., AND K. J. BABBITT. 2014. Amphibian contributions to ecosystem services. Herpetological Conservation and Biology 9:1–17.

HOLOMUZKI, J. R., J. P. COLLINS, AND P. E. BRUNKOW 1994. Trophic control of fishless ponds by tiger salamander larvae. Oikos 71:55–64.

IUCN (INTERNATIONAL UNION OF CONSERVATION OF NATURE). 2014. The IUCN Red List of Threatened Species. Version 2014.1. Available at http://www.iucnredlist.org. Archived by WebCite at http://www.webcitation.org/5KY30olNh on 20 November 2006.

KEITZER, S. C., AND R. R. GOFORTH. 2013. Salamander diversity alters stream macroinvertebrate community structure. Freshwater Biology 58:2114–2125.

LANNOO, M. J. 2005. Amphibian declines: the conservation status of United States species. University of California Press, Berkely, CA, USA.

MERRITT, R. W., K. W. CUMMINS, AND M. B. BERG 2008. An introduction to the aquatic insects of North America. 4th ed. Kendall Hunt Publishing Company, Dubuque, USA.

MORIN, P. J. 1981. Predatory salamanders reverse the outcome of competition among three species of anuran tadpoles. Science 212:1284–1286.

MULLINS, M. L., B. A. PIERCE, AND K. J. GUTZWILLER. 2004. Assessment of quantitative enclosure sampling of larval amphibians. Journal of Herpetology 38:166–173.

O'BRIEN, W. J., N. A. SLADE, AND G. L. VINYARD. 1976. Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*). Ecology 57:1304–1310.

OUSTERHOUT, B. H., T. L. ANDERSON, D. L. DRAKE, W. E. PETERMAN, AND R. D. SEMLITSCH. 2015. Habitat traits and species interactions differentially affect abundance and body size in pond-breeding amphibians. Journal of Animal Ecology 84:914–924.

PETERKA, J., AND J. MATENA. 2009. Differences in feeding electivity and efficiency between young-of-the-year European perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*)—field observations and laboratory experiments on the importance of prey movement apparency vs. evasiveness. Biologia 64:786–794.

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.

REGESTER, 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.

REISSIG, M., C. QUEIMALIÑOS, B. MODENUTTI, AND E. BALSEIRO. 2015. Prey C: P ratio and phosphorus recycling by a planktivorous fish: advantages of fish selection towards pelagic cladocerans. Ecology of Freshwater Fish 24:214–224.

SCHRIEVER, T. J., M. W. CADOTTE, AND D. D. WILLIAMS. 2014. How hydroperiod and species richness affect the balance of resource flows across aquatic–terrestrial habitats. Aquatic Sciences 76:131–143.

SEALE, D. B. 1980. Influence of amphibian larvae on primary production, nutrient flux, and competition in a pond ecosystem. Ecology 616:1531–1550.

SEALE, D. B., AND N. BECKVAR. 1980. The comparative ability of anuran larvae genera: (*Hyla*, *Bufo* and *Rana*) to ingest suspended blue-green algae. Copeia 1980 (3):495–503.

THORP, J. H., AND A. P. COVICH [EDS]. 2001. Ecology and classification of North American freshwater invertebrates. 2nd ed. Academic Press, USA.

TURNER, A. M., AND G. G. MITTELBACH. 1990. Predator avoidance and community structure: interactions among piscivores, planktivores, and plankton. Ecology, 71:2241–2254.

VAN BUSKIRK, J., AND D. SMITH. 1991. Density-dependent population regulation in a salamander. Ecology 725:1747–1756. doi:10.2307/1940973.

WALLS, S. C. 1995. Differential vulnerability to predation and refuge use in competing larval salamanders. Oecologica 101:86–93.

WERNER, E., D. SKELLY, R. RELYEA, AND K. YUREWICZ. 2007. Amphibian species richness across environmental gradients. Oikos 116:1697–1712.

WHILES, M. R., J. B. JENSEN, J. G. PALIS, AND W. G. DYER. 2004. Diets of larval flatwoods salamanders, *Ambystoma cingulatum*, from Florida and South Carolina. Journal of Herpetology 38:208–214.

WHILES, M. R., R. O. HALL, W. K. DODDS, P. VERBURG, A. D. HURYN, C. M. PRINGLE, K. R. LIPS, S. S. KILHAM, C. COLON-GAUD, A. T. RUGENSKI, ET AL. 2013. Disease-driven amphibian declines alter ecosystem processes in a tropical stream. Ecosystems 16:146–157.

WISSINGER, S. A., A. J. BOHONAK, H. H. WHITEMAN, AND W. S. BROWN. 1999. Subalpine wetlands in Colorado: habitat permanence, salamander predation, and invertebrate communities. Pp. 757–790 in Invertebrates in Freshwater Wetlands of North America: Ecology and Management. Wiley, New York, USA.