

ARTICLE

Freshwater Ecology

Limited population and community effects of hatching asynchrony in a pond-breeding salamander

Thomas L. Anderson¹  | Jacob J. Burkhardt¹  | Jacob A. Cianci-Gaskill²  | Jon M. Davenport¹ 

¹Department of Biology, Appalachian State University, Boone, North Carolina, USA

²School of Natural Resources, University of Missouri, Columbia, Missouri, USA

Correspondence

Thomas L. Anderson
Email: thander@siue.edu

Present address

Thomas L. Anderson, Department of Biological Sciences, Southern Illinois University Edwardsville, Edwardsville, Illinois 62026, USA.

Jacob A. Cianci-Gaskill, Ohio Department of Natural Resources, Huron, Ohio 44839, USA.

Funding information

U.S. Department of Defense, Grant/Award Number: SERDP RC-2703

Handling Editor: Bryan L. Brown

Abstract

Understanding attributes of phenology beyond the mean date of a life history event, such as variability among individuals within a population, is critical to predict how climate-induced phenological shifts may alter population dynamics. Identifying how phenological variability impacts organisms is especially needed to better understand how phenological shifts affect trophic dynamics (e.g., shifts in variability of top predators affecting primary production). To better understand the effects of phenological variability on both populations and communities, we examined how variation in egg hatching synchrony of predatory marbled salamanders (*Ambystoma opacum*) impacted intraspecific interactions at the larval stage, ultimately affecting demographic traits and survival through metamorphosis. We also examined how hatching synchrony affected overall trophic dynamics (e.g., primary consumers and producers) in pond food webs. We experimentally manipulated the degree of hatching synchrony of embryonic *A. opacum* and subsequently reared larvae in outdoor mesocosms. We monitored demographic traits such as larval growth, size at and time to metamorphosis, and survival. To assess trophic dynamics, we monitored zooplankton abundance and phytoplankton biomass during the experiment. Larvae exhibited greater variability in body size in medium and low hatching synchrony treatments compared to high synchrony treatments. Larval body size variation diminished over time to ultimately result in no differences in most life history traits at metamorphosis or survival among hatching synchrony treatments. We also found no differences among treatments in zooplankton abundance or phytoplankton biomass, likely because of minimal variation in *A. opacum* survival among treatments that would induce top-down changes. Overall, we found that phenological variation may be context dependent in its influence on demography and overall community structure. Because of concerns for how phenological shifts will affect species interactions, greater scrutiny into conditions that would promote changes in population and community dynamics is needed.

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2023 The Authors. *Ecosphere* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

KEYWORDS

amphibian, cannibalism, growth rate, phenology, pond, predation, synchrony

INTRODUCTION

The timing of different life history events, or phenology, is changing for many species worldwide (Cohen et al., 2018; Parmesan, 2007). It is expected that such changes will lead to altered population and community dynamics by affecting the magnitude of intra- and interspecific interactions (Miller-Rushing et al., 2010; Nakazawa & Doi, 2012; Yang & Rudolf, 2010). Shifts in species interactions are likely to occur through processes such as the well-established match–mismatch scenario, where the phenologies of consumers and their required resources become desynchronized (Cushing, 1990; McKinney et al., 2012). Additionally, phenological shifts can affect which size classes or stages interact within or between species, altering the outcome of those interactions and ultimately affecting life history, demographic rates, and coexistence (Rudolf, 2019; Yang & Rudolf, 2010). Yet, mechanistic tests that unravel how species interactions will unfold with some degree of phenological change are uncommon (e.g., Carter & Rudolf, 2019; Kudo & Cooper, 2019; Rafferty & Ives, 2011), in part because it is not always clear how different phenological metrics will affect species interactions.

The most commonly investigated phenological metrics include the first, mean, or median date of the expression of a phenological trait (Forrest & Miller-Rushing, 2010; Inouye et al., 2019), which are either benchmarks of only one individual in that population (e.g., first date) or uninformative about the within-season variability among individuals in phenology (e.g., the mean or median). Phenological metrics that describe the variability of the entire phenological distribution (e.g., degree of variability or skewness) have received less attention (Anderson, Earl, et al., 2021), despite variability being equally likely to impact populations via shifts in species interactions (Forrest & Miller-Rushing, 2010). In the studies that have examined such metrics, they have found considerable effects on the outcome of interactions with con- and heterospecifics. For instance, increasing phenological variability of individuals of the same species around a given mean date magnified the strength of intraspecific priority effects in anurans, with early-arriving individuals outcompeting later-arriving cohorts (Rasmussen & Rudolf, 2015). Additionally, the degree to which individuals within a population exhibit reproductive synchrony (i.e., low variability) can influence their susceptibility to predators across a wide range of taxa via predator swamping (Ims, 1990). In some cases, shifting variability can be as or

more important than shifts in the phenological mean in shaping species interactions (Carter & Rudolf, 2019; Rasmussen & Rudolf, 2016). Because different phenological metrics can change independently (CaraDonna et al., 2014) and likely differentially affect populations and communities, a more thorough understanding of different types of phenological shifts is needed, especially those beyond mean or first date of an event.

Investigations into whether shifts in phenology affect species interactions have focused primarily on pairwise interactions (e.g., match–mismatch scenarios; Cushing, 1990). However, most species are often embedded within complex food webs, with the potential for any effects of individual phenological shifts to be transmitted across trophic levels (Both et al., 2009; Nakazawa & Doi, 2012). Trophic-level impacts of phenological shifts may be especially prevalent if the magnitude of shift and subsequent population response is substantial and/or the species exhibiting the shift in phenology plays a critical role in food webs (e.g., a keystone species). These scenarios of phenological shifts, among others, may scale up or down to affect overall community structure, creating the potential for a phenology-dependent trophic cascade. Phenological variability that results in a large amount of body size variability may particularly affect communities, as it has been noted to influence communities across trophic levels in other studies (Crumrine, 2010a; Rudolf & Rasmussen, 2013).

Amphibians have well-documented changes in phenology, especially for metrics like the first or median date of breeding activity (Blaustein et al., 2001; Lunghi, 2018; Todd et al., 2011). Other measures of phenology are less well understood, though several recent experiments have begun to unravel how factors like the degree of hatching synchrony affect amphibian dynamics (Anderson et al., 2020; Carter & Rudolf, 2019; Rasmussen & Rudolf, 2015, 2016). There is also a substantial body of literature on how the timing of breeding and/or hatching impacts species interactions through intra- and interspecific priority effects (Boone et al., 2002; Lawler & Morin, 1993; Murillo-Rincón et al., 2017; Rudolf, 2022; Wilbur & Alford, 1985). For predaceous species, body size variability generated through differences in hatching phenology can initiate intra- and interspecific predation, depending on the relative size advantages early-hatching individuals have over later-hatching individuals (Eitam et al., 2005; Griffiths et al., 1994; Kishida et al., 2011; Segev & Blaustein, 2007). However, some amphibians can also offset delays in breeding by exhibiting compensatory growth in the larval stage,

sometimes incurring costs in life history traits or physiology (Burraco et al., 2020; Dahl et al., 2012), and depending on their relative breeding order (Murillo-Rincón et al., 2017). Compensatory growth can also occur with apparently limited negative consequences on life history traits (Anderson et al., 2017; Orizaola et al., 2010). Because amphibians often fill critical roles as top predators in pond food webs (Morin, 1995; Wilbur et al., 1983), shifts in phenology in those species may also have cascading effects across other trophic levels.

The goal of this study was to assess how egg hatching synchrony of a top predator influenced its life history traits and whether such effects were transmitted to other trophic levels. We addressed this goal using *Ambystoma opacum* (marbled salamander), a pond-breeding species known for initiating strong top-down effects in aquatic food webs during its larval stage (Davenport & Chalcraft, 2012; Morin, 1995; Stemp et al., 2021; Urban, 2013). We specifically addressed two questions: (1) How does variation in hatching synchrony affect intraspecific interactions in a top predator? and (2) How does hatching synchrony in a top predator alter other trophic levels (e.g., primary consumers and producers). Our work builds on previous tests of phenological synchrony in that we examined variation in hatching synchrony that each spanned equivalent time periods (6 weeks) centered around a mean date, as compared to differences in synchrony that spanned different durations (e.g., Rasmussen & Rudolf, 2015). In general, we found an absence of strong intraspecific interactions on predator traits and survival, which led to limited effects across the entire food web.

METHODS

Study system

Ambystoma opacum occurs across much of the eastern United States (Lannoo, 2005). Adults breed in the fall, laying eggs in terrestrial nests along the margins of ephemeral to semipermanent wetlands. Eggs then hatch into aquatic larvae after inundation by rising water levels (Petranka & Petranka, 1981). Larvae overwinter in ponds prior to undergoing metamorphosis in late spring to early summer. Larval diet primarily consists of zooplankton, other invertebrates, and larvae of other amphibians (Branch & Altig, 1981; Petranka & Petranka, 1980; Stemp et al., 2021). Larvae are also known to be highly aggressive and cannibalistic on conspecifics, especially if size variation among individuals exists (Mott & Maret, 2011; Smith, 1990; Walls & Blaustein, 1995). Larval *A. opacum* are top predators in fishless ponds, influencing both

amphibian and invertebrate communities (Davenport & Chalcraft, 2012; Morin, 1995; Stemp et al., 2021; Urban, 2013). Recent evidence in South Carolina has shown that the median breeding date for *A. opacum* has also shifted to 15 days later than the historical median date (Todd et al., 2011), suggesting larvae would have a smaller body size in the spring and a reduced role as a top predator (Urban, 2007) unless compensatory growth occurs.

Variability in the degree of hatching synchrony would be expected to occur for *A. opacum* because not all individuals lay nests at the same height in a pond basin and because ponds often fill incrementally (Petranka & Petranka, 1981). Thus, individual nests would be potentially flooded at different times, depending on the amount of rainfall that occurs within a given period of time. If rainfall amounts are lower and/or more infrequent, only nests at the lowest elevation would be initially inundated. As more rainfall accumulates, the remaining nests would be inundated, leading to asynchrony in hatching. Thus, with increased variability in rainfall, hatching asynchrony may become more likely. In contrast, in years where greater amounts of rain occur within a short period of time, all nests may become inundated simultaneously, leading to greater hatching synchrony.

Experimental design

We assessed the importance of hatching synchrony variation by implementing three treatments that all had equal salamander densities: high synchrony (36 hatchlings added on one date), medium synchrony (12 hatchlings added on each of three dates), and low synchrony (6 hatchlings added on each of six dates; Appendix S1: Figure S1). The additions for the medium and low synchrony treatments were each centered on the high synchrony treatment addition date and were each spread across a period of 6 weeks (Appendix S1: Figure S1). One tank inadvertently received 37 hatchlings instead of 36; inclusion or exclusion of this tank did not influence our results, so we left it in the analysis. We also included a control treatment, which received no hatchling *A. opacum*, to assess how the absence of top predators affected our experimental food webs. All synchrony treatments had six replicates, while the control treatment had three replicates. All treatments were randomly assigned within one large experimental array.

Experimental set-up

We conducted the experiment in outdoor mesocosms (1000-L cattle watering tanks; hereafter, tanks) at the

University of Missouri from October 2018 to June 2019. We filled tanks with water in late September and let tanks sit for ~7 days to allow chlorine to evaporate. We added 1 kg of dry leaf litter (primarily *Quercus* sp., *Carya* sp., and *Platanus occidentalis*) and ~1.5 L of concentrated pond water from nearby natural areas to each tank to initiate plankton communities that served as the base of the food web. Tanks were uncovered throughout the experiment to permit natural colonization by prey insects, such as dipterans. Predatory invertebrates (e.g., dragonflies) were not observed to have colonized tanks, likely because the experiment took place primarily over the winter months when such species are not active.

We collected ~15 nests of *A. opacum* from seven populations at Fort Leonard Wood, Missouri, on 3 and 18 October 2018. We housed the nests on moist soil and moss within plastic containers in an environmentally controlled room (18°C, ~60% humidity, 12:12 light:dark cycle). We evenly distributed clutches across each addition date to minimize genetic influences. To initiate hatching, we flooded eggs with tank water approximately 1 week before their addition date. Addition dates were centered on 8 November, with 21 October and 26 November being the earliest and last additions, respectively (Appendix S1: Figure S1). We haphazardly caught hatchlings for each addition and added them to the assigned tanks.

To assess larval size variation, we captured larvae using aquarium nets from each tank at four time points during development: 6 January, 13 March, 3 April, and 23 April. Larvae were dorsally photographed in a pan with water and a ruler. We obtained measurements of total length, head width (HW), snout–vent length (SVL; approximated as the distal junction of the hind limbs and tail), and maximum girth across the torso. Here, we report on larval HW, as all metrics were highly correlated (all $r > 0.93$). We did not record mass to minimize handling time of larvae. Sample sizes per tank varied by date due to reduced activity by larvae and limited visibility in the upper water column as spring progressed, but always included at least eight individuals per tank (range: 8–16).

We added two species of prey salamanders to all tanks in early April 2019 to evaluate how phenological synchrony affected intraguild interactions and overall food web dynamics. We added 15 hatchling *Ambystoma texanum* on 3 April and 15 hatchling *Ambystoma maculatum* on 12 April to each mesocosm. We did not measure hatchling size for these taxa, but they are sufficiently small enough to be consumed by multiple size classes of larval *A. opacum* at this time of year (Anderson et al., 2016). As evidence of this, only one *A. maculatum* and zero *A. texanum* survived in tanks with *A. opacum*, and so we did not analyze these data. In the control

treatment, average survival was 89% for *A. texanum* and 93% for *A. maculatum*.

We began checking the surface of the water and the lip of each tank at least every other day for metamorphosing animals in early May 2019. Each tank had an inverted end to the lip, thus ensuring mortality was not confounded with animals escaping prior to capture. We removed individuals that had reabsorbed their gills and recorded their mass (in grams) and date of metamorphosis. We again dorsally photographed individuals over a ruler to obtain the same measurements as above. In early June, we drained all tanks and carefully sifted through the leaf litter to find any remaining individuals; no *A. opacum* were found, meaning they had all metamorphosed or died. We determined survival of *A. opacum* by tallying the number of metamorphs per tank.

We sampled the zooplankton community from each mesocosm on 19 March, 9 April, and 1 May 2019. On each date, we pooled four water column samples, one from each cardinal direction of the tank. Samples were collected using an integrated sampler that was submerged from just above the leaf litter. We then filtered the consolidated sample (~2.5 L) through an 80- μm net. We anesthetized zooplankton with sodium bicarbonate (Alka Seltzer tablets), and preserved samples in 50% isopropyl alcohol. We categorized and counted zooplankton as cladocerans, copepods, and rotifers under a dissecting microscope, and calculated the total abundance across all groups.

We estimated algal biomass by measuring chlorophyll *a* (chl *a*) concentrations from phytoplankton and periphyton from each mesocosm on 20 March, 9 April, and 1 May 2019. On each date, we pooled four integrated water samples, one from each cardinal direction of the tank, into a single sample bottle. Water was homogenized by inverting the sample bottle and was then filtered onto a 1.0- μm A/E glass fiber filter within 2 h of collection. In November 2018, we attached three 47 \times 47 mm ceramic plates to the wall of each tank to measure periphyton chl *a*. On each sampling date listed above, a plate was removed, cleaned with a wire brush, and rinsed onto a 1.0 μm A/E glass fiber filter. All filters, both for phytoplankton and periphyton, were frozen at -20°C until analysis (within 3 months), at which point chl *a* was extracted with heated ethanol, phaeophytin acid-corrected, and measured fluorometrically with a Turner Design Fluorometer (TD-700) following established procedures (Knowlton, 1984; Sartory & Grobbelaar, 1984). The reporting limit for chl *a* quantification was 0.9 $\mu\text{g L}^{-1}$.

Analysis

All analyses were conducted in R v4.2.1 (R Core Team, 2022). For the larval stage, we calculated both the

mean and CV ($SD \times \text{mean}^{-1}$; hereafter, “variability”) of HW for all captured individuals in each tank on each date. We used linear mixed-effects models from the “nlme” package to analyze how both the mean and variability in HW changed across treatments through time (Pinheiro et al., 2022). For both responses, we included treatment, linear and quadratic terms of day of year (DOY), interaction terms between DOY and treatment as fixed effects, and tank as a random effect to account of repeated sampling of tanks. Because individuals were not marked, we could not statistically control for the repeated measurement of some individuals that would have occurred over time. We initially compared models that included DOY and tank as random slope and intercept terms, respectively, against a model with only random intercepts for tanks. Likelihood ratio tests indicate random slopes were not supported and were removed from the model for each response (all $p > 0.05$). Significance of the linear and quadratic terms was based on whether confidence intervals overlapped zero.

For metamorphs, we again calculated tank means and CV for traits at metamorphosis (SVL, mass, and DOY). We used general linear models to analyze each of the six response variables, with synchrony treatment as a categorical predictor (i.e., ANOVA). We did not analyze larval period duration as individuals were not identifiable from each addition, leaving the true duration unknown except in the high synchrony treatment. We analyzed survival using a generalized linear model with quasibinomial errors to correct for overdispersion, again with treatment as the only predictor. Significance was assessed using the “Anova” function from the “car” package in R (Fox & Weisberg, 2011). If treatment was significant, we examined treatment differences using Tukey post hoc tests in the “emmeans” package (Lenth, 2022).

For zooplankton abundance (total and each group separately), phytoplankton biomass, and periphyton biomass, we again used linear mixed models (Pinheiro et al., 2022). For all models, we included synchrony treatment and date as fixed effects, their interaction, and tank as a random effect. The interaction term would indicate whether plankton samples differed before or after the alternative prey salamanders (*A. texanum* and *A. maculatum*) were added to tanks, as they could have altered those trophic levels, especially in the controls. However, the interaction term was not significant in any model and was thus removed, though we further confirmed these patterns by analyzing each date separately, as the 20 March sample was taken prior to prey salamander addition and the remaining two samples after prey salamander (Appendix S1). We log-transformed zooplankton abundances to improve normality of the residuals. Significance was again assessed using the

“Anova” function from the “car” package (Fox & Weisberg, 2011). As above, we examined significant treatment and date differences using Tukey post hoc tests.

RESULTS

Larval growth

Mean larval HW increased nonlinearly through time but did not vary by treatment (Figure 1a; Table 1). In contrast, variability in HW showed strong differences among treatments that changed nonlinearly with time (Figure 1b; Table 1). Both the low and medium synchrony treatments initially showed high levels of variability in HW, with some individuals nearly double the size of other individuals within the same tank (Appendix S1: Figure S2). However, such variation declined through time, ultimately converging to have the same degree of variability as the high synchrony treatment by the last sampling date (Figure 1b; Appendix S1: Figure S2). The high synchrony treatment showed only a slight increase in variability through time (Figure 1b).

Metamorphosis

Hatching synchrony treatments did not affect average SVL, mass, or date of metamorphosis (Figure 2a–c; Table 2). Overall, average survival of *A. opacum* was high (>72% in all tanks). There was moderate evidence that survival was affected by hatching synchrony, with the medium synchrony treatment being lower than the high treatment (Figure 2d; Table 2). The odds of a larva surviving were 4.7 times lower in the medium treatment than in the high (odds ratio = 0.21). There was no evidence that variability in SVL or mass at metamorphosis differed between treatments, but there was strong evidence that variability in date of metamorphosis was lower in the high synchrony treatment compared the medium and low treatments (Figure 3; Table 2), that is, synchrony in metamorphosis was greater when hatching was more synchronized.

Community effects

There was no evidence that phytoplankton chl *a* concentrations differed between synchrony treatments (Appendix S1: Figure S3), though each treatment had higher concentrations than the control (Table 3). There was strong evidence that phytoplankton concentrations differed by sampling date (Table 3). There was no evidence that periphyton chl *a* concentrations varied among

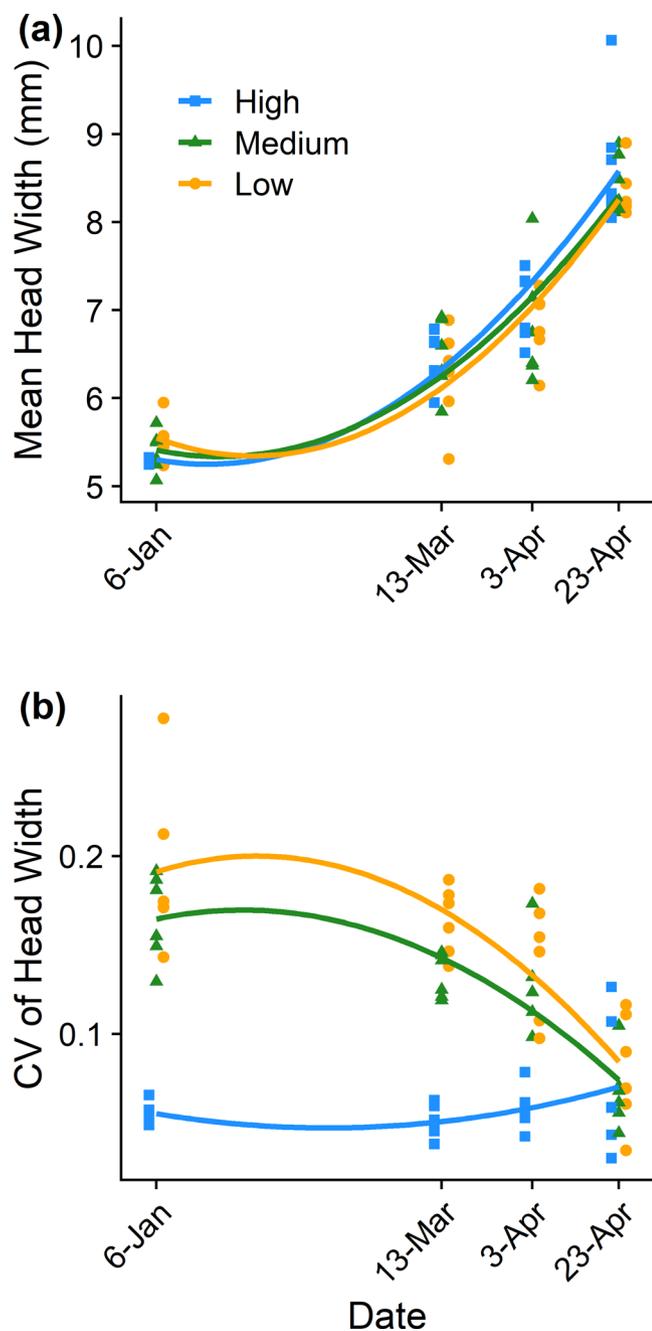


FIGURE 1 Mean (a) and CV (b) in head width of larval *Ambystoma opacum* across four sampling dates in each synchrony treatment (symbols and colors). Each point represents the average (a) or CV (b) of a mesocosm. Points are adjusted horizontally to minimize overlap. Lines indicate predicted values based on a model with linear and quadratic effects of day of year.

any of the treatments, but strong evidence that they did vary by date (Table 3; Appendix S1: Figure S3). Similarly, there was no evidence that total zooplankton abundance and each individual groups' abundance (cladocerans, copepods, and rotifers) varied by treatment, but there was strong evidence that they did vary by date (Table 3; Appendix S1: Figure S3).

DISCUSSION

Phenological shifts are expected to impact population and community dynamics, in part by affecting species interactions (Yang & Rudolf, 2010). However, the importance of such changes is difficult to predict because examinations of how shifts other than the mean date of an event, such as variability, affect ecological systems are still relatively rare. Here, we observed that the degree of hatching synchrony had minimal effects on average life history traits (body size and development) and only affected survival of a top predator, *A. opacum*. Synchrony treatments also affected the CV in the timing of metamorphosis, with reduced variation in this trait for the high synchrony treatment. Because of the minimal effects of phenological variation on survival of *A. opacum*, and thus predator density, among treatments, we also observed limited differences in food webs among treatments. Therefore, while there is evidence that phenological variation strongly alters species interactions for some taxa (Carter & Rudolf, 2019; Rasmussen & Rudolf, 2015, 2016), we show that is not always the case.

Numerous studies have linked phenological shifts to altered species interactions, both in experimental and observational settings (Kharouba et al., 2018). In particular, altered hatching synchrony can result in highly asymmetric intra- and interspecific species interactions for many aquatic organisms due to increased body size disparities that shift interactions from scramble to contest competition or increase predation rates (Boone et al., 2002; Carter & Rudolf, 2019; Eitam et al., 2005; Kishida et al., 2011; Murillo-Rincón et al., 2017; Rasmussen et al., 2014; Rasmussen & Rudolf, 2015; Segev & Blaustein, 2007; Van Buskirk, 1992). In contrast to this body of work, we found only survival varied among treatments; traits such as average body size or timing of metamorphosis did not differ among treatments. Even survival only differed by approximately 10% among the high and medium synchrony treatments—effects consistent with four individuals being consumed. We unfortunately were not able to track cohorts as in other studies (Ryan & Plague, 2004), so it is unclear which cohort contributed most to this survival difference. This difference in survival between treatments is consistent with our introduction patterns: the medium synchrony treatment had the largest time duration between when cohorts were added, increasing the possibility of predation, whereas the low synchrony treatment had continuous and less extreme time differences between additions. The low and medium synchrony treatments had identical initial and final introduction dates, each spanning a six-week period, which may explain why the treatment differences were not more substantial. Rasmussen and Rudolf (2015) manipulated synchrony over different

TABLE 1 Summary statistics for linear mixed-effects models of mean and CV in larval head width through time.

Type	Parameter	Value	SE	df	<i>t</i>	<i>p</i>	Lower CI	Upper CI
Mean	Intercept	5.590	0.165	52	34	<0.001	5.260	5.930
	Low	−0.105	0.189	15	−0.554	0.588	−0.507	0.298
	Medium	−0.144	0.189	15	−0.764	0.457	−0.547	0.258
	DOY	−0.017	0.005	52	−3.64	<0.001	−0.026	−0.008
	DOY ²	0.0004	0.00004	52	9.36	<0.001	0.0003	0.0005
CV	Intercept	0.058	0.012	48	4.71	<0.001	0.033	0.083
	Low	0.103	0.017	15	5.92	<0.001	0.066	0.140
	Medium	0.128	0.017	15	7.35	<0.001	0.091	0.165
	DOY	−0.0005	0.0005	48	−0.967	0.338	−0.001	0.0005
	DOY ²	0.00001	0.000004	48	1.23	0.224	−0.000003	0.00001
	Low DOY	0.00112	0.000679	48	1.65	0.106	−0.0002	0.002
	Medium DOY	0.00143	0.000679	48	2.11	0.040	0.0001	0.003
	Low DOY ²	−0.00002	0.000006	48	−3.03	0.004	−0.00003	−0.00001
	Medium DOY ²	−0.00002	0.000006	48	−3.69	<0.001	−0.00003	−0.00001

Note: Fixed effects were synchrony treatment and day of year (DOY; linear and quadratic terms), with tank as a random effect. An interaction effect between DOY and treatment was initially included but was not significant and removed from the mean response. Values are reported as the effects parameterization, with the high synchrony treatment as the reference (Intercept) level. The *p* values in boldface indicate significant effects. Results in text are discussed in terms of evidence, as outlined in Muff et al. (2022).

time ranges, which may have contributed to their larger differences in survival.

We observed that variability in the timing of metamorphosis was related to the degree of hatching synchrony: when hatching was synchronous, there was lower variability in the date of metamorphosis. The degree to which phenological events are coupled for a given organism varies widely among taxa—some species show strong coherence between events, whereas others show weak or absent patterns (Augspurger & Zaya, 2020; CaraDonna et al., 2014). Such convergence in the timing of metamorphosis in salamanders is important for population dynamics because early emigration from wetlands is tied to increased adult fitness (Semlitsch et al., 1988). If climate change increases rainfall variability during the breeding season as predicted (Pendergrass et al., 2017), we hypothesize that subsequent changes in the timing of when individuals emigrate from wetlands could occur, leading to increased exposure to aquatic predators and risk of desiccation from the pond drying prematurely and ultimately affecting population dynamics. Additionally, for species that rely on synchronized phenology as an anti-predator behavior as they emigrate from wetlands (DeVito, 2003), such ontogenetic changes in hatching may lessen the effectiveness of this behavior if it reduces how many individuals transition at a given time. More generally, as the degree of reproductive synchrony is a common phenomenon across many taxa (Ims, 1990; Warkentin, 2011), a greater understanding of how such

patterns affect subsequent phenological events in those organisms life history (e.g., flowering synchrony on timing of senescence) is needed, especially in the context phenological shifts associated with climate change.

Trophic cascades are common in aquatic systems (Chase, 2000), and larval salamanders have been shown to initiate them when they serve as top predators in the food web (Blaustein et al., 1996; Holomuzki et al., 1994). Here, we found little support for cascading effects because our treatments did not strongly affect salamander survival, which we had expected would lead to a density-dependent trophic cascade. Because survival did not vary substantially, no cascading effects were transmitted to other trophic levels, though we did observe phytoplankton biomass to be lower in the control treatment. Zooplankton abundance did not vary statistically across any treatments, however, making the phytoplankton differences not consistent with a trophic cascade. The lack of trophic effects could be due to the stochastic nature of plankton population dynamics, our limited sampling of the community may have provided insufficient power to uncover any treatment effects on these taxa (even if present), or the addition of the prey salamanders that altered the community patterns from the expected trophic cascade. Nonetheless, further studies are needed to evaluate how phenological shifts will impact multiple trophic levels, as such multitrophic interactions are often context-dependent and subject to density- or trait-mediated effects.

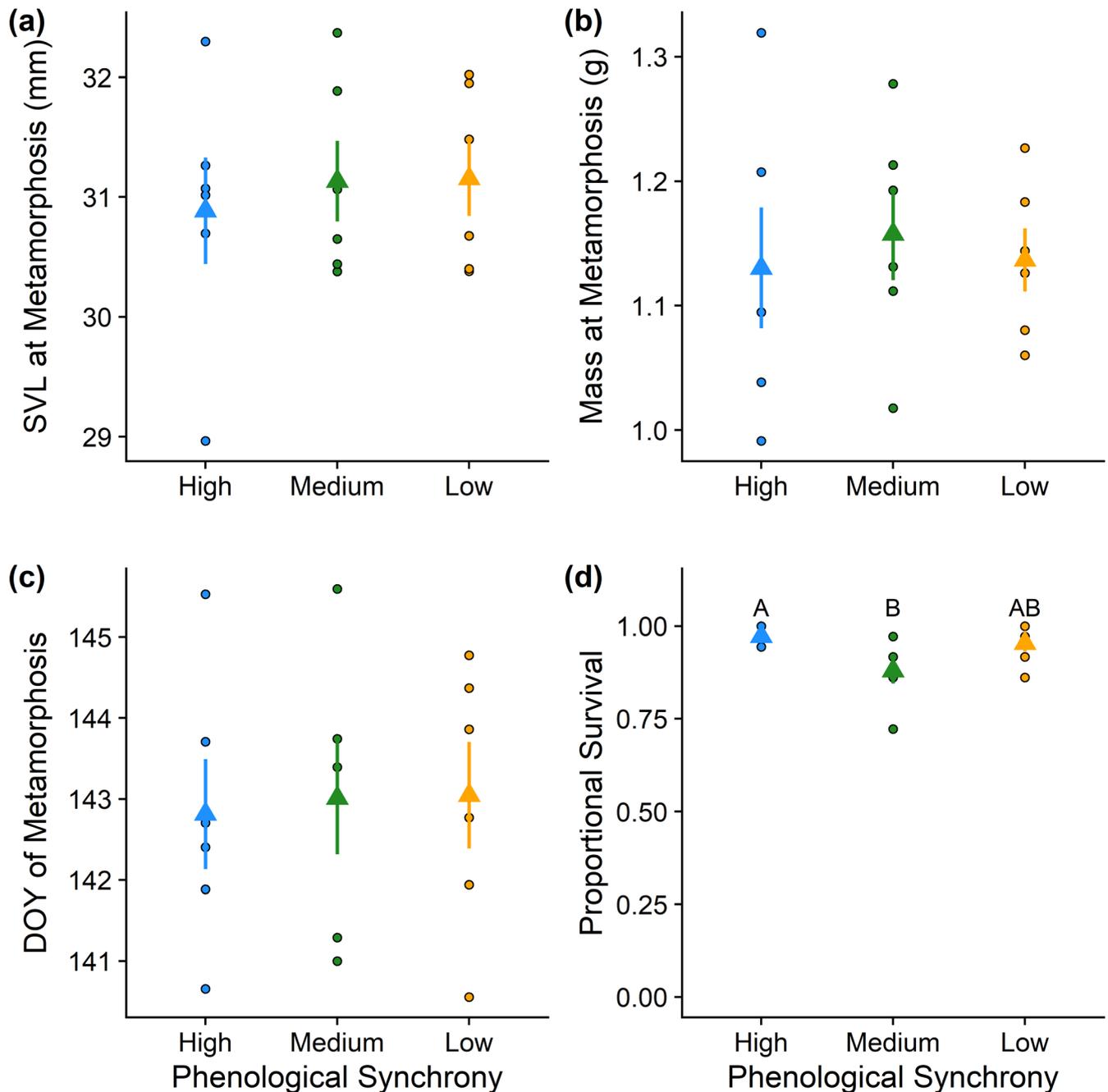


FIGURE 2 Snout-vent length (SVL; a), mass (b), day of year (DOY) at metamorphosis (c), and survival (d) of *Ambystoma opacum* for each phenological synchrony treatment. Circles represent tank averages (a–c) or totals (d). Triangles and lines represent treatment means \pm SE. Letters above treatments in (d) indicate significant treatment differences based on Tukey contrasts. No treatment differences were significant for any response in (a)–(c).

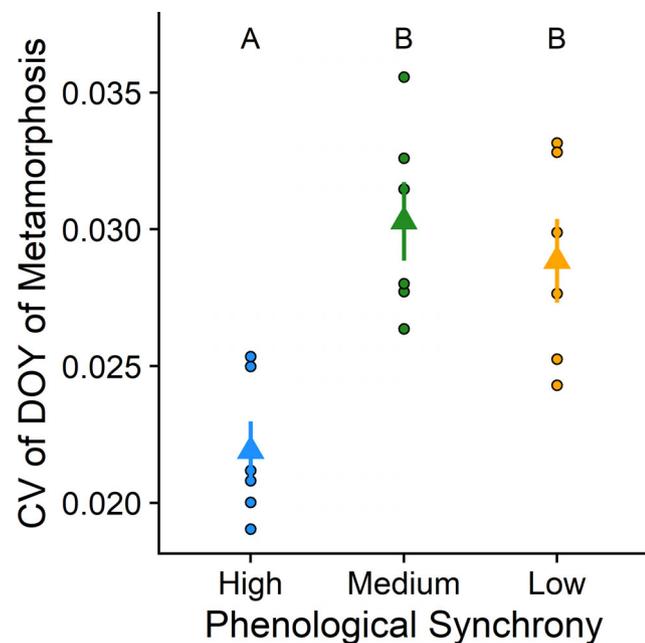
Except for survival and CV of metamorphosis, treatment effects were absent across all other salamander and food web responses. These results were surprising because we observed a high degree of variability in body size among salamanders when hatching was asynchronous, especially early in the experiment, and size-structured populations of consumers often exhibit high levels of cannibalism and/or interference

competition (Miller & Rudolf, 2011; Wilbur, 1988). In particular, the medium and high synchrony treatments produced individuals that were nearly double the body size of other individuals in the same tank. Based on previous work (Anderson et al., 2013; Rasmussen et al., 2014; Wissinger et al., 2010), this size difference would suggest that cannibalism and interference should have been prevalent, as has been noted in other *A. opacum* studies (Petranka, 1989).

TABLE 2 Summary statistics for mean and CV models at metamorphosis for *Ambystoma opacum*.

Response type	Response	F	df	p
Mean	SVL	0.164	2	0.851
	Mass	0.139	2	0.871
	DOY	0.034	2	0.967
	Survival	4.290	2	0.034
CV	SVL	0.128	2	0.881
	Mass	1.757	2	0.206
	DOY	10.851	2	0.001

Note: General linear models (i.e., ANOVA) were used for mean and CV of snout-vent length (SVL), mass, and day of year (DOY) of metamorphosis. We used a generalized linear model with quasibinomial errors for survival. Statistics for survival are generated from approximate *F* tests using Kenward-Roger df. There were 15 residual df in all models. The *p* values in boldface indicate significant effects. Results in text are discussed in terms of strength of evidence (Muff et al., 2022).

**FIGURE 3** CV in day of year (DOY) of metamorphosis in *Ambystoma opacum*. Circles represent average values for a tank. Triangles and lines represent treatment means \pm SE. Letters indicate treatment differences based on Tukey contrasts.

However, we did not observe cannibalism, as discussed above. We hypothesize three potential reasons for the minimal differences in survival among treatments. First, while salamander densities were near the median range of values reported for natural populations (Petranka, 1989; Scott, 1990) and some individuals had tail damage that would indicate attempts at cannibalism, encounter rates may still not have been high enough to result in substantial cannibalism or interference. Second, prey densities (e.g.,

TABLE 3 Summary statistics for linear mixed-effects models for phytoplankton biomass, periphyton biomass, total zooplankton abundance, cladoceran abundance, copepod abundance, and rotifer abundance.

Response	Factor	χ^2	df	p
Phytoplankton	Treatment	14.7	3	0.002
	Date	52.6	2	<0.001
Periphyton	Treatment	2.07	3	0.559
	Date	22.4	2	<0.001
Zooplankton	Treatment	2.22	3	0.527
	Date	11.2	2	0.003
Cladocerans	Treatment	1.71	3	0.634
	Date	14.2	2	0.001
Copepods	Treatment	0.76	3	0.858
	Date	22.9	2	<0.001
Rotifers	Treatment	3.83	3	0.28
	Date	55.6	2	<0.001

Note: Fixed effects were synchrony treatment and day of year. Tank was a random effect. There were 15 residual df in all models. The *p* values in boldface indicate significant effects. Results in the text are discussed in terms of strength of evidence (Muff et al., 2022).

zooplankton and other invertebrates) may have been high enough to satiate larval *A. opacum*, resulting in low rates of cannibalism and interference. Hopper et al. (1996) similarly found that only low food levels lead to high rates of cannibalism among larval dragonflies. Third, a lack of strong differences in survival across treatments could have occurred because low water temperature reduced activity rates, of cannibalism and interference (Crumrine, 2010b). *Ambystoma opacum* breeds in the fall, and thus its larvae experience a cooling thermal environment, as opposed to the many spring-breeding species with larvae that experience warming water temperatures as spring progresses. Because of their breeding seasonality, if *A. opacum* larvae hatch late enough in the season, they may only experience cooler water temperatures that would limit activity and growth. Our experiment started in late October, and thus early additions may have had lower activity rates and metabolisms, resulting in foraging on less prey that are less mobile prey than salamanders. Breeding seasons shifted earlier in the fall, when water temperatures are warmer, may initiate higher levels of predation among different breeding cohorts (Anderson, Burkhart, & Davenport, 2021).

One possible explanation for our lack of differences among individual traits is compensatory growth (Metcalf & Monaghan, 2001)—individuals that were added later converged on similar body sizes and timing of metamorphosis. We suspect compensatory growth occurred here

as the larval duration must have been reduced for some individuals that had delayed phenologies, given that (1) there was no difference in the date of metamorphosis among treatments and (2) the degree of variability in hatching was substantially higher (6 weeks) than the duration of metamorphosis (~6 days), meaning the variation was not maintained across phenological events. This accelerated growth ultimately resulted in no differences in length and mass at metamorphosis, indicating minimal costs to such growth, similar to other studies (Anderson et al., 2017; Orizaola et al., 2010). Unfortunately, we could not track actual per capita growth rates and true larval period lengths due to the inability to identify individuals/cohorts, which would be needed to provide evidence for this hypothesis. Overall, the adaptive potential to enact compensatory growth and reduce future costs due to phenological shifts is a promising avenue of research to explore further when considering whether populations will show resilience against climate change.

Our lack of strong evidence on the importance of phenological shifts highlight an important caveat to phenological research—phenological shifts may be context dependent, with many abiotic or biotic axes explaining such variation (Chmura et al., 2019). Such contexts could be similar to the ideas discussed above, such as temperature dependence, or include things like nutrient levels or the identity of the organisms involved (Rudolf, 2022; Rudolf & McCrory, 2018). Consideration of how phenological variation is manifested may be critical, such as whether the distribution of events is skewed or kurtotic in pattern, or if the time spans over which variation occurs are of similar or different durations. Additionally, the timescale of phenological shifts relative to the life history of the organism may be important. Our treatments spanned a 42-day period, which matches the natural breeding duration of *A. opacum* (Timm et al., 2007). However, the larval duration of *A. opacum* is over 200 days; the degree of variation in breeding may simply not matter given the long duration over which individuals can overcome any initial differences. When phenological shifts encompass a greater percentage of the typical duration of the subsequent life stage (e.g., a 15-day shift for a life stage that only occurs for 30 days), such shifts have a much greater effect on life history traits or survival, as observed in Rasmussen and Rudolf (2015).

Many species have exhibited shifts in phenology (Parmesan, 2007), and there has been growing concern that such changes will impact species interactions and demography (Miller-Rushing et al., 2010; Nakazawa & Doi, 2012; Yang & Rudolf, 2010). However, causal links between phenological shifts and changes in species interactions or community dynamics remain to be demonstrated in many species or ecosystems. Even within a

given taxonomic grouping, not all species will be equally affected by phenological shifts. For example, life history traits and survival of some amphibians are clearly affected by changes in phenology (Boone et al., 2002; Carter & Rudolf, 2019; Rasmussen & Rudolf, 2015), whereas in other amphibians this relationship is more ambiguous (Alford, 1989; Anderson et al., 2017, 2020). Therefore, further investigation into when and how species interactions will be disrupted by phenological change and whether such shifts in interactions cascade across multiple trophic levels are clearly needed.

ACKNOWLEDGMENTS

We thank the Division of Biological Sciences and M. Leal at the University of Missouri for support and access to facilities; K. Stemp, J. Hardy, S. Sheth, A. Maddox, A. Knutson, A. Ward, and J. Kent for helping collect and measure metamorphs; A. Babineau, H. Shoptaugh, and A. Bricchetto for counting zooplankton. Animals were collected with Missouri Department of Conservation approval (#17673), and experiments were conducted with Institutional Animal Care and Use Committee approval (Missouri: #9297; Appalachian State: #18-19).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Anderson et al., 2022) are available from Zenodo: <https://doi.org/10.5281/zenodo.6967637>.

ORCID

Thomas L. Anderson  <https://orcid.org/0000-0001-7479-2192>

Jacob J. Burkhart  <https://orcid.org/0000-0002-7913-6220>

Jacob A. Cianci-Gaskill  <https://orcid.org/0000-0002-6778-6170>

Jon M. Davenport  <https://orcid.org/0000-0002-9911-2779>

REFERENCES

- Alford, R. A. 1989. "Variation in Predator Phenology Affects Predator Performance and Prey Community Composition." *Ecology* 70: 206–19.
- Anderson, T. L., J. J. Burkhart, J. A. Cianci-Gaskill, and J. M. Davenport. 2022. "Data from: Limited Population and Community Effects of Hatching Asynchrony in a Pond-Breeding Salamander." Zenodo. <https://doi.org/10.5281/zenodo.6967637>.
- Anderson, T. L., J. J. Burkhart, and J. M. Davenport. 2021. "Asymmetric Density-Dependent Competition and Predation between Larval Salamanders." *Freshwater Biology* 66: 1356–65.

- Anderson, T. L., J. E. Earl, D. J. Hocking, M. S. Osbourn, T. A. G. Rittenhouse, and J. R. Johnson. 2021. "Demographic Effects of Phenological Variation in Natural Populations of Two Pond-Breeding Salamanders." *Oecologia* 196: 1073–83.
- Anderson, T. L., C. Linares, K. N. Dodson, and R. D. Semlitsch. 2016. "Variability in Functional Response Curves among Larval Salamanders: Comparisons across Species and Size Classes." *Canadian Journal of Zoology* 94: 23–30.
- Anderson, T. L., C. L. Mott, T. D. Levine, and H. H. Whiteman. 2013. "Life Cycle Complexity Influences Intraguild Predation and Cannibalism in Pond Communities." *Copeia* 2013: 284–91.
- Anderson, T. L., F. E. Rowland, and R. D. Semlitsch. 2017. "Variation in Phenology and Density Differentially Affects Predator–Prey Interactions between Salamanders." *Oecologia* 185: 475–86.
- Anderson, T. L., K. M. Stemp, B. H. Ousterhout, D. Burton, and J. M. Davenport. 2020. "Impacts of Phenological Variability in a Predatory Larval Salamander on Pond Food Webs." *Journal of Zoology* 310: 95–105.
- Augsburger, C. K., and D. N. Zaya. 2020. "Concordance of Long-Term Shifts with Climate Warming Varies among Phenological Events and Herbaceous Species." *Ecological Monographs* 90: e01421.
- Blaustein, A. R., L. K. Belden, D. H. Olson, D. M. Green, T. L. Root, and J. M. Kiesecker. 2001. "Amphibian Breeding and Climate Change." *Conservation Biology* 15: 1804–9.
- Blaustein, L., J. Friedman, and T. Fahima. 1996. "Larval *Salamandra* Drive Temporary Pool Community Dynamics: Evidence from an Artificial Pool Experiment." *Oikos* 76: 392–402.
- Boone, M. D., D. E. Scott, and P. H. Niewiarowski. 2002. "Effects of Hatching Time for Larval Ambystomatid Salamanders." *Copeia* 2002: 511–7.
- Both, C., M. Van Asch, R. G. Bijlsma, A. B. Van Den Burg, and M. E. Visser. 2009. "Climate Change and Unequal Phenological Changes across Four Trophic Levels: Constraints or Adaptations?" *Journal of Animal Ecology* 78: 73–83.
- Branch, L. C., and R. Altig. 1981. "Nocturnal Stratification of Three Species of *Ambystoma* Larvae." *Copeia* 1981: 870–3.
- Burraco, P., A. E. Valdés, and G. Orizaola. 2020. "Metabolic Costs of Altered Growth Trajectories across Life Transitions in Amphibians." *Journal of Animal Ecology* 89: 855–66.
- CaraDonna, P. J., A. M. Iler, and D. W. Inouye. 2014. "Shifts in Flowering Phenology Reshape a Subalpine Plant Community." *Proceedings of the National Academy of Sciences* 111: 4916–21.
- Carter, S. K., and V. H. W. Rudolf. 2019. "Shifts in Phenological Mean and Synchrony Interact to Shape Competitive Outcomes." *Ecology* 100: e02826.
- Chase, J. M. 2000. "Are there Real Differences among Aquatic and Terrestrial Food Webs?" *Trends in Ecology & Evolution* 15: 408–12.
- Chmura, H. E., H. M. Kharouba, J. Ashander, S. M. Ehlman, E. B. Rivest, and L. H. Yang. 2019. "The Mechanisms of Phenology: The Patterns and Processes of Phenological Shifts." *Ecological Monographs* 89: e01337.
- Cohen, J. M., M. J. Lajeunesse, and J. R. Rohr. 2018. "A Global Synthesis of Animal Phenological Responses to Climate Change." *Nature Climate Change* 8: 224–8.
- Crumrine, P. W. 2010a. "Size-Structured Cannibalism between Top Predators Promotes the Survival of Intermediate Predators in an Intraguild Predation System." *Journal of the North American Benthological Society* 29: 636–46.
- Crumrine, P. W. 2010b. "Body Size, Temperature, and Seasonal Differences in Size Structure Influence the Occurrence of Cannibalism in Larvae of the Migratory Dragonfly, *Anax junius*." *Aquatic Ecology* 44: 761–70.
- Cushing, D. 1990. "Plankton Production and Year-Class Strength in Fish Populations: An Update of the Match/Mismatch Hypothesis." *Advances in Marine Biology* 26: 249–93.
- Dahl, E., G. Orizaola, A. G. Nicieza, and A. Laurila. 2012. "Time Constraints and Flexibility of Growth Strategies: Geographic Variation in Catch-up Growth Responses in Amphibian Larvae." *Journal of Animal Ecology* 81: 1233–43.
- Davenport, J. M., and D. R. Chalcraft. 2012. "Evaluating the Effects of Trophic Complexity on a Keystone Predator by Disassembling a Partial Intraguild Predation Food Web: Disassembling a Partial Intraguild Predation Food Web." *Journal of Animal Ecology* 81: 242–50.
- DeVito, J. 2003. "Metamorphic Synchrony and Aggregation as Antipredator Responses in American Toads." *Oikos* 103: 75–80.
- Eitam, A., L. Blaustein, and M. Mangel. 2005. "Density and Intercohort Priority Effects on Larval *Salamandra salamandra* in Temporary Pools." *Oecologia* 146: 36–42.
- Forrest, J., and A. J. Miller-Rushing. 2010. "Toward a Synthetic Understanding of the Role of Phenology in Ecology and Evolution." *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 3101–12.
- Fox, J., and S. Weisberg. 2011. *An R Companion to Applied Regression*, 2nd ed. Thousand Oaks, CA: Sage.
- Griffiths, R. A., P. de Wijer, and R. T. May. 1994. "Predation and Competition within an Assemblage of Larval Newts (*Triturus*)." *Ecography* 17: 176–81.
- Holomuzki, J. R., J. P. Collins, and P. E. Brunkow. 1994. "Trophic Control of Fishless Ponds by Tiger Salamander Larvae." *Oikos* 71: 55–64.
- Hopper, K. R., P. H. Crowley, and D. Kielman. 1996. "Density Dependence, Hatching Synchrony, and within-Cohort Cannibalism in Young Dragonfly Larvae." *Ecology* 77: 191–200.
- Ims, R. A. 1990. "The Ecology and Evolution of Reproductive Synchrony." *Trends in Ecology & Evolution* 5: 135–40.
- Inouye, B. D., J. Ehrlén, and N. Underwood. 2019. "Phenology as a Process Rather than an Event: From Individual Reaction Norms to Community Metrics." *Ecological Monographs* 89: e01352.
- Kharouba, H. M., J. Ehrlén, A. Gelman, K. Bolmgren, J. M. Allen, S. E. Travers, and E. M. Wolkovich. 2018. "Global Shifts in the Phenological Synchrony of Species Interactions over Recent Decades." *Proceedings of the National Academy of Sciences* 115: 5211–6.
- Kishida, O., G. C. Trussell, A. Ohno, S. Kuwano, T. Ikawa, and K. Nishimura. 2011. "Predation Risk Suppresses the Positive Feedback between Size Structure and Cannibalism: Predation Risk and Cannibalism." *Journal of Animal Ecology* 80: 1278–87.
- Knowlton, M. F. 1984. "Flow-through Microcuvette for Fluorometric Determination of Chlorophyll." *Journal of the American Water Resources Association* 20: 795–9.

- Kudo, G., and E. Cooper. 2019. "When Spring Ephemerals Fail to Meet Pollinators: Mechanism of Phenological Mismatch and Its Impact on Plant Reproduction." *Proceedings of the Royal Society B: Biological Sciences* 286: 20190573.
- Lannoo, M. J. 2005. *Amphibian Declines: The Conservation Status of United States Species*. Berkeley, CA: University of California Press.
- Lawler, S. P., and P. J. Morin. 1993. "Temporal Overlap, Competition, and Priority Effects in Larval Anurans." *Ecology* 74: 174–82.
- Lenth, R. 2022. "emmeans: Estimated Marginal Means, aka Least-Squares Means." R Package Version 1.8.0. <https://CRAN.R-project.org/package=emmeans>.
- Lunghi, E. 2018. "Comparative Reproductive Biology of European Cave Salamanders (Genus *Hydromantes*): Nesting Selection and Multiple Annual Breeding." *Salamandra* 54: 101–8.
- McKinney, A. M., P. J. CaraDonna, D. W. Inouye, B. Barr, C. D. Bertelsen, and N. M. Waser. 2012. "Asynchronous Changes in Phenology of Migrating Broad-Tailed Hummingbirds and their Early-Season Nectar Resources." *Ecology* 93: 1987–93.
- Metcalfe, N. B., and P. Monaghan. 2001. "Compensation for a Bad Start: Grow Now, Pay Later?" *Trends in Ecology & Evolution* 16: 254–60.
- Miller, T. E. X., and V. H. W. Rudolf. 2011. "Thinking inside the Box: Community-Level Consequences of Stage-Structured Populations." *Trends in Ecology & Evolution* 26: 457–66.
- Miller-Rushing, A. J., T. T. Høye, D. W. Inouye, and E. Post. 2010. "The Effects of Phenological Mismatches on Demography." *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 3177–86.
- Morin, P. J. 1995. "Functional Redundancy, Non-Additive Interactions, and Supply-Side Dynamics in Experimental Pond Communities." *Ecology* 76: 133–49.
- Mott, C. L., and T. J. Maret. 2011. "Species-Specific Patterns of Agonistic Behavior among Larvae of Three Syntopic Species of Ambystomatid Salamanders." *Copeia* 2011: 9–17.
- Muff, S., E. B. Nilsen, R. B. O'Hara, and C. R. Nater. 2022. "Rewriting Results Sections in the Language of Evidence." *Trends in Ecology & Evolution* 37: 203–10.
- Murillo-Rincón, A. P., N. A. Kolter, A. Laurila, and G. Orizaola. 2017. "Intraspecific Priority Effects Modify Compensatory Responses to Changes in Hatching Phenology in an Amphibian." *Journal of Animal Ecology* 86: 128–35.
- Nakazawa, T., and H. Doi. 2012. "A Perspective on Match/Mismatch of Phenology in Community Contexts." *Oikos* 121: 489–95.
- Orizaola, G., E. Dahl, and A. Laurila. 2010. "Compensating for Delayed Hatching across Consecutive Life-History Stages in an Amphibian." *Oikos* 119: 980–7.
- Parmesan, C. 2007. "Influences of Species, Latitudes and Methodologies on Estimates of Phenological Response to Global Warming." *Global Change Biology* 13: 1860–72.
- Pendergrass, A. G., R. Knutti, F. Lehner, C. Deser, and B. M. Sanderson. 2017. "Precipitation Variability Increases in a Warmer Climate." *Scientific Reports* 7: 1–9.
- Petranka, J. W. 1989. "Density-Dependent Growth and Survival of Larval *Ambystoma*: Evidence from Whole-Pond Manipulations." *Ecology* 70: 1752–67.
- Petranka, J. W., and J. G. Petranka. 1980. "Selected Aspects of the Larval Ecology of the Marbled Salamander *Ambystoma opacum* in the Southern Portion of its Range." *American Midland Naturalist* 104: 352–63.
- Petranka, J. W., and J. G. Petranka. 1981. "On the Evolution of Nest Site Selection in the Marbled Salamander, *Ambystoma opacum*." *Copeia* 1981: 387–91.
- Pinheiro, J., D. Bates, and R Core Team. 2022. "nlme: Linear and Nonlinear Mixed Effects Models." R Package Version 3.1-158. <https://CRAN.R-project.org/package=nlme>.
- R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Rafferty, N. E., and A. R. Ives. 2011. "Effects of Experimental Shifts in Flowering Phenology on Plant-Pollinator Interactions: Experimental Shifts in Flowering Phenology." *Ecology Letters* 14: 69–74.
- Rasmussen, N. L., and V. H. W. Rudolf. 2015. "Phenological Synchronization Drives Demographic Rates of Populations." *Ecology* 96: 1754–60.
- Rasmussen, N. L., and V. H. W. Rudolf. 2016. "Individual and Combined Effects of Two Types of Phenological Shifts on Predator–Prey Interactions." *Ecology* 97: 3414–21.
- Rasmussen, N. L., B. G. Van Allen, and V. H. W. Rudolf. 2014. "Linking Phenological Shifts to Species Interactions through Size-Mediated Priority Effects." *Journal of Animal Ecology* 83: 1206–15.
- Rudolf, V. H. W. 2019. "The Role of Seasonal Timing and Phenological Shifts for Species Coexistence." *Ecology Letters* 22: 1324–38.
- Rudolf, V. H. W. 2022. "Temperature and Nutrient Conditions Modify the Effects of Phenological Shifts in Predator–Prey Communities." *Ecology* 13: e3704.
- Rudolf, V. H. W., and S. McCrory. 2018. "Resource Limitation Alters Effects of Phenological Shifts on Inter-Specific Competition." *Oecologia* 188: 515–23.
- Rudolf, V. H. W., and N. L. Rasmussen. 2013. "Ontogenetic Functional Diversity: Size Structure of a Keystone Predator Drives Functioning of a Complex Ecosystem." *Ecology* 94: 1046–56.
- Ryan, T. J., and G. R. Plague. 2004. "Hatching Asynchrony, Survival, and the Fitness of Alternative Adult Morphs in *Ambystoma talpoideum*." *Oecologia* 140: 46–51.
- Sartory, D., and J. Grobbelaar. 1984. "Extraction of Chlorophyll a from Freshwater Phytoplankton for Spectrophotometric Analysis." *Hydrobiologia* 114: 177–87.
- Scott, D. E. 1990. "Effects of Larval Density in *Ambystoma opacum*: An Experiment Large-Scale Field Enclosures." *Ecology* 71: 296–306.
- Segev, O., and L. Blaustein. 2007. "Priority Effects of the Early Breeding Fire Salamander on the Late Breeding Banded Newt." *Hydrobiologia* 583: 275–83.
- Semlitsch, R. D., D. E. Scott, and J. H. K. Pechmann. 1988. "Time and Size at Metamorphosis Related to Adult Fitness in *Ambystoma talpoideum*." *Ecology* 69: 184–92.
- Smith, C. K. 1990. "Effects of Variation Body Size on Intraspecific Competition among Larval Salamanders." *Ecology* 71: 1777–88.
- Stemp, K. M., T. L. Anderson, and J. M. Davenport. 2021. "Macrogeographic Variation of a Pond Predator's Top-Down Effects in a Common Garden Environment." *Population Ecology* 63: 5–13.
- Timm, B. C., K. McGarigal, and B. W. Compton. 2007. "Timing of Large Movement Events of Pond-Breeding Amphibians in

- Western Massachusetts, USA.” *Biological Conservation* 136: 442–54.
- Todd, B. D., D. E. Scott, J. H. K. Pechmann, and J. W. Gibbons. 2011. “Climate Change Correlates with Rapid Delays and Advancements in Reproductive Timing in an Amphibian Community.” *Proceedings of the Royal Society B: Biological Sciences* 278: 2191–7.
- Urban, M. C. 2007. “Predator Size and Phenology Shape Prey Survival in Temporary Ponds.” *Oecologia* 154: 571–80.
- Urban, M. C. 2013. “Evolution Mediates the Effects of Apex Predation on Aquatic Food Webs.” *Proceedings of the Royal Society B: Biological Sciences* 280: 20130859.
- Van Buskirk, J. 1992. “Competition, Cannibalism, and Size Class Dominance in a Dragonfly.” *Oikos* 65: 455–64.
- Walls, S. C., and A. R. Blaustein. 1995. “Larval Marbled Salamanders, *Ambystoma opacum*, Eat their Kin.” *Animal Behaviour* 50: 537–45.
- Warkentin, K. M. 2011. “Environmentally Cued Hatching across Taxa: Embryos Respond to Risk and Opportunity.” *Integrative and Comparative Biology* 51: 14–25.
- Wilbur, H. M. 1988. “Interactions between Growing Predators and Growing Prey.” In *Size-Structured Populations*, edited by B. Ebenman and L. Persson, 157–72. Cham: Springer.
- Wilbur, H. M., and R. A. Alford. 1985. “Priority Effects in Experimental Pond Communities: Responses of *Hyla* to *Bufo* and *Rana*.” *Ecology* 66: 1106–14.
- Wilbur, H. M., P. J. Morin, and R. N. Harris. 1983. “Salamander Predation and the Structure of Experimental Communities: Anuran Responses.” *Ecology* 64: 1423–9.
- 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: 549–59.
- Yang, L. H., and V. H. W. Rudolf. 2010. “Phenology, Ontogeny and the Effects of Climate Change on the Timing of Species Interactions.” *Ecology Letters* 13: 1–10.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Anderson, Thomas L., Jacob J. Burkhart, Jacob A. Cianci-Gaskill, and Jon M. Davenport. 2023. “Limited Population and Community Effects of Hatching Asynchrony in a Pond-Breeding Salamander.” *Ecosphere* 14(2): e4372. <https://doi.org/10.1002/ecs2.4372>