



# Refilling temporary ponds has timing-dependent effects on *Hyla gratiosa* performance

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**Abstract**

1. Disturbances and variation in abiotic habitat conditions greatly affect populations and communities. The multitude of processes that occur in natural systems offers the possibility that the trajectories of ephemeral habitats and the effects of disturbances can be slowed or reversed. Hydroperiod is a defining characteristic in freshwater systems, with temporary ponds supporting distinct communities of organisms with plastic developmental trajectories and complex lifecycles that allow them to cope with the vagaries of pond duration.
2. Despite work on the effects of pond drying on aquatic animals, little consideration has been given to filling, which can extend the duration of small, drying ponds. Our goal was to assess how increasing the volume of small ponds affects the developmental trajectories of larval amphibians living in these habitats. We conducted a field mesocosm experiment to assess how filling of ponds early, midway and late in the larval period affected the survival and development of the barking treefrog, *Hyla gratiosa*. We hypothesised that filling early in the larval stage would provide the most benefits, producing more and larger metamorphs than filling later in development.
3. We found that through various effects on survival, metamorphosis, habitat quality and competition, increasing volume early in development produced more and larger metamorphs with faster growth rates than any other treatment, whereas filling late in development produced few, small, slow growing metamorphs.
4. Our results provide support for the role of stressors in initiating metamorphosis and also show that increased pond volumes early in larval development can provide benefits to *Hyla* populations in terms of compensatory growth, but filling late in development has little benefit.

**KEYWORDS**

amphibian, compensatory growth, disturbance, habitat duration, life history

## 1 | INTRODUCTION

Habitat duration and disturbance frequency are dominant drivers of community composition, population structure and individual fitness across landscapes in a diverse array of systems (Chesson, 2000; Hobbs & Huenneke, 1992; Schneider, 1997; Sousa, 1984). Effects of changing habitat quality can be both direct and indirect, with lethal

direct effects often appearing more dramatic through the wholesale loss or catastrophic alteration of an existing habitat and resulting direct mortality of its inhabitants (Glitzenstein, Platt, & Streng, 1995; Glynn, 1993; Wilbur, 1997). However, indirect effects can have both abiotic and biotic components, as well as lethal and non-lethal effects, which alter intraspecific and interspecific interactions through either changes in abundances of species or shifts in the

competitive balance between interacting species (Chalcraft & Andrews, 1999; Rogers & Chalcraft, 2008; Sousa, 1984; Wootten, 1994). For surviving individuals in particular, it is ultimately these indirect effects that affect fitness and shape community structure through changing cues that initiate life history events, movement from patches and completion of critical life stages (Denver, 1997b; Newman, 1987; Pfennig, 1990; Skúlason & Smith, 1995).

Habitat duration has often been viewed as a contingent process; there are typically temporal components to environmental processes that dictate the persistence of habitats (Newman, 1988; Schneider & Frost, 1996). This is particularly true in freshwater systems, where the duration of freshwater habitats is determined by their hydroperiod—the amount of time that they retain water. The transition from permanent to temporary water bodies is a defining characteristic of freshwater habitats (Wellborn, Skelly, & Werner, 1996), and there has been considerable work on the effects of hydroperiod on a diverse group of freshwater organisms. In drying ponds, studies of insects and amphibians have demonstrated that metamorphosis occurs earlier and at smaller body sizes as hydroperiod decreases (Juliano & Stoffregen, 1994; Laurila & Kujasalo, 1999; Newman, 1988; Pechmann, Scott, Gibbons, & Semlitsch, 1989; Schäfer & Lundström, 2006; Semlitsch & Wilbur, 1988; Skelly, 1996; Tejedo & Reques, 1994; Waterkeyn, Grillas, Vanschoenwinkel, & Brendonck, 2008; Wilbur, 1987). Although earlier metamorphosis allows individuals to avoid desiccation, the resulting smaller body sizes can have consequences for future fitness, as larger individuals have higher breeding success, produce more offspring and have better overwinter survival (Berven, 1981; Berven & Gill, 1983; Semlitsch, Scott, & Pechmann, 1988; Smith, 1987).

This deterministic view of hydroperiod and pond drying is not representative of the range of outcomes that can occur in natural systems. Pond drying is not always a one-way process, as precipitation and/or flooding can refill ponds at any point in the course of drying, not only after a pond has completely dried. Refilling can provide numerous benefits by increasing pond volume and surface area, reducing conspecific density, and importing nutrients and other resources that can support higher productivity. Conversely, flooding can introduce competitors or predators, particularly fish, from nearby habitats that can have detrimental effects on organisms typically found in temporary ponds (Hartel et al., 2007; Hecnar & M'Closkey, 1997; Teplitsky, Plénet, & Joly, 2003; Thomaz, Bini, & Bozelli, 2007). Plants in communities within and around ponds are adapted to certain hydrologic regimes, and divergence from normal hydroperiods through either filling or rapid drying can have negative effects (Coops & Van der Velde, 1995; Poiani & Johnson, 1989). Following dormant periods, inundation of dry habitats surrounding ponds can cause the acceleration of biogeochemical reactions and biological processes, resulting in large fluxes of nutrients that persist for short time durations immediately after filling (McClain et al., 2003; McKnight et al., 1999; Stanley, Fisher, & Jones, 2004). Organisms with complex lifecycles inhabiting temporary ponds have the plasticity to respond to pond drying, so we would expect they can also change developmental trajectory after refilling to maximise benefits

gained from growth opportunities in refilled ponds or, conversely, further speed up development to escape impacts of introduced predators.

Thus, refilling has the potential to drastically alter communities and change the development and life history trajectories of organisms in temporary ponds. However, the degree of plasticity exhibited by larval amphibians is in part dependent on developmental stage. Individual plasticity in response to environmental changes is greater early in larval development and less so later in development (Leips & Travis, 1994; Relyea, 2003), and once metamorphosis begins, changes to the developmental trajectory are unlikely (Newman, 1992; Wilbur & Collins, 1973). Our goal was to assess the effects of timing of filling small ponds on larval *Hyla gratiosa* (barking treefrog) development and survival, while eliminating other factors confounded with flooding (nutrients, predators, etc.). Because larval anurans are more responsive to changes early in development, we hypothesised that filling early in the larval stage would be the most beneficial, producing more and larger metamorphs than other treatments.

## 2 | METHODS

Our experiment was conducted in a field with open canopy at the University of Mississippi Field Station (UMFS) in Lafayette County, Mississippi, USA. On 17 April 2014 mesocosms (plastic cattle tanks: 1.8 m diameter, ~1,300 L;  $N = 40$ ) were filled with water (filtered through 1.13-mm fibreglass mesh) from a nearby pond. We measured out 2-kg aliquots of dry hardwood leaf litter (primarily *Quercus* spp.) and randomly assigned these aliquots to each mesocosm as a nutrient base to support primary and secondary productivity. Adjustable standpipes were affixed to mesocosms to maintain desired water levels, and each mesocosm was covered with a tight-fitting fibreglass screen lid (1.13 mm opening) to prevent the escape of metamorphs, the entry of unwanted colonists and the addition of other organic matter (e.g. tree leaf litter). In early June 2014, we collected amplexed *Hyla gratiosa* pairs at UMFS and placed them in plastic containers with water overnight. The following morning adult treefrogs were released, and the eggs were taken to the lab to hatch.

Within one day of hatching, we sorted individuals from each clutch into aliquots of 20 and randomly assigned these aliquots to aggregate groups of 300 assigned to individual mesocosms. The 300 larvae were sourced from at least four separate clutches, and all clutches within each block were from eggs laid on the same night. Larvae were added to mesocosms as they were sorted (from 13 to 16 June), by block, with larvae added to two blocks per day. Block was also the position of mesocosms from west to east (in a  $5 \times 8$  array), and consisted of five mesocosms, with the five treatments randomly assigned within each block. Thus, block simultaneously accounted for any spatial variation in environmental conditions and variation due to the date on which eggs were laid.

Treatment was the time at which each mesocosm was refilled. One treatment, “full,” served as a positive control and started at the maximum depth for each mesocosm (52 cm) and remained so throughout the experiment. A second treatment, “low,” was a negative control and remained at the minimum depth of 15 cm (28.8% of the maximum) for the duration of the experiment. A natural pond with a depth of 15 cm could easily dry in two months or less during the summer in our system, so a mesocosm of that depth would be expected to provide sufficient cues of a risky environment and greater competition among larval inhabitants for fewer resources in a smaller volume. The remaining three treatments began at a depth of 15 cm, but were then filled with water from the same source pond at one of three different intervals: 15, 30 or 45 days after larvae were added to each mesocosm. These times represent filling occurring early, midway and late, respectively, in the typical two-month larval period (ranging from 1.2 to 5.3 months) of *H. gratiosa* (Altig & McDiarmid, 2015; Leips, McManus, & Travis, 2000; Travis, 1983a, 1984; Wright, 1932). These three filling treatments were maintained at full depth for the duration of the experiment after filling. None of the mesocosms ever actually dried, and we maintained constant volumes in all mesocosms by topping off with well water as needed during summer. Well water at UMFS is chemically similar to rain water (relative to mesocosm water; Pintar & Resetarits, 2017), and allowed us to maintain volumes without introducing additional cues or organisms from source ponds. At full volumes, larval densities in our experiment were representative of typical natural larval anuran densities we have observed at UMFS and used in other experiments using *H. gratiosa* (Travis, 1983a,b; Wilbur, 1982). Low volumes represented an extreme, but not unrealistic, high density of larvae.

Once larvae were added, we checked each mesocosm daily for metamorphs, which were collected, weighed and released near source ponds at UMFS. Metamorphs were also photographed in standardised positions (with scales for calibration) in ImageJ to measure snout-urostyle length (SUL; Schneider, Rasband, & Eliceiri, 2012). On 4–7 November, we collected and counted all remaining larvae by block in the same manner as larvae were added. We only used these surviving larvae for determining overall survival throughout the experiment, but we present additional size and developmental data of these larvae in the supporting information (Appendix S1). All surviving larvae were returned to a fishless pond immediately after processing. The experiment was terminated on 7 November 2014.

## 2.1 | Data analysis

We used a series of analyses to assess the effects of filling on *H. gratiosa* survival and metamorph size, growth and larval period length. Means of all individuals in each mesocosm were used to analyse larval size and metamorph size, growth and larval period and avoid pseudoreplication. All analyses used type III SS,  $\alpha = 0.05$  and were conducted in R v.3.4.3 (R Core Team, 2017). We conducted post hoc comparisons only when the main effect of treatment was  $p < 0.05$  using Fisher's Protected LSD, with  $\alpha = 0.05$  for individual

LSD comparisons. Data are available in figshare (Pintar & Resetarits, 2018a).

### 2.1.1 | Survival

For survival, we analysed the effect of treatment using logistic regression in two separate analyses on (a) the proportion of metamorphs and (b) overall survival in each mesocosm (metamorphs + surviving larvae). The metamorph analysis included the overall number of surviving individuals as a fixed covariate to account for potential intraspecific competition. Both logistic regressions used a binomial error distribution with mesocosm nested within treatment as random effects to correct for overdispersion (Warton & Hui, 2011).

### 2.1.2 | Metamorphs

We did not necessarily expect correlated responses among all metamorph variables, and therefore analysed the effects on metamorph body condition, growth rate, larval period, mass and SUL separately using linear mixed effects models in the lme4 package v 1.1-15 (Bates, Mächler, Bolker, & Walker, 2015). All metamorph analyses included block as a random factor, and we tested for significance with approximate *F* tests (Type III Satterthwaite) in the lmerTest package v 2.0-36 (Kuznetsova, Brockhoff, & Christensen, 2017). In these metamorph analyses, survival and larval period were square root transformed ( $\sqrt{X + 0.5}$ ), and SUL and mass were log transformed.

We analysed metamorph mass and SUL with mixed effects models using overall survival as a covariate and treatment as a fixed factor. Metamorph body condition (size-independent mass) was analysed by mean-scaling mass to decouple variance from the measurement scale and means, regressing against SUL and using the residuals in a mixed effects model with overall survival as a covariate and treatment as a fixed factor (Berner, 2011). We analysed the length of the larval period (days to metamorphosis after egg laying) with a mixed effects model that included overall survival as a covariate and block and treatment as factors. Metamorph growth rate (mm/day) was calculated by dividing metamorph SUL by days to metamorphosis and analysed with treatment as a fixed factor and overall survival as a covariate in a mixed effects model. Two mesocosms produced only one metamorph each (all other mesocosms had at least six metamorphs), so they were excluded from metamorph size analyses ( $N = 35$ ; also excluding mesocosms with zero metamorphs), but maintained in survival analyses ( $N = 40$ ). In metamorph size analyses, all treatments had at least six replicates.

## 3 | RESULTS

### 3.1 | Survival

There was a significant effect of treatment on overall survival ( $\chi^2_4 = 9.68$ ,  $p = 0.0462$ ; Figure 1). “Low” mesocosms (depth of 15 cm throughout experiment) had the lowest survival, and “full”

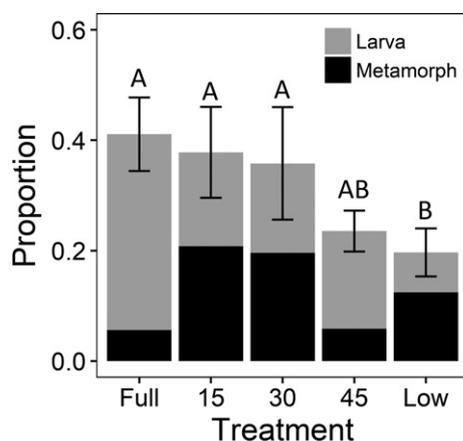
mesocosms (depth of 52 cm throughout experiment) and those filled from 15 to 52 cm after 15 and 30 days the highest overall survival. We observed a significant effect of treatment on the proportion of metamorphs (Table 1). “Full” mesocosms produced the fewest metamorphs, and “low” mesocosms and those filled after 15 and 30 days produced the most metamorphs (Figure 2a). This metamorph pattern likely contributed to the covariance of overall survival with many metamorph measurements and some larval measurements.

### 3.2 | Metamorphs

Metamorph body condition was not affected by treatment and did not covary with survival (Table 1; Figure 2b). Metamorph growth rate was affected by treatment, but not overall survival: metamorph growth rate was higher in mesocosms filled after 15 days than any other treatments (Table 1; Figure 2c). Metamorphs began to emerge on 9 July and continued to do so until 30 October; however, length of the larval period was not affected by treatment, but did covary with survival (Table 1). The average time it took to reach metamorphosis ranged by approximately three weeks (Figure 2d), and length of the larval period was shorter when survival was higher. Larval period length was initially included as a covariate in other analyses, as prolonging the larval period can enable individuals to reach larger sizes (Wilbur & Collins, 1973). However, it was not a significant covariant in any analysis ( $p > 0.5$ ), and we excluded it. Metamorph mass and SUL were affected by treatment and covaried with survival (Table 1; Figure 2e,f). Metamorphs were largest in mesocosms filled after 15 days and smallest in the “low” mesocosms and those filled at 30 and 45 days, whereas those in “full” mesocosms were intermediate. Metamorphs were also larger in mesocosms with lower overall survival (Table 1).

## 4 | DISCUSSION

The creation and persistence of habitat patches and their constituent communities, along with the role of disturbance, have been central



**FIGURE 1** Average proportion of individuals surviving (larvae + metamorphs) in each treatment (means  $\pm$  SE)

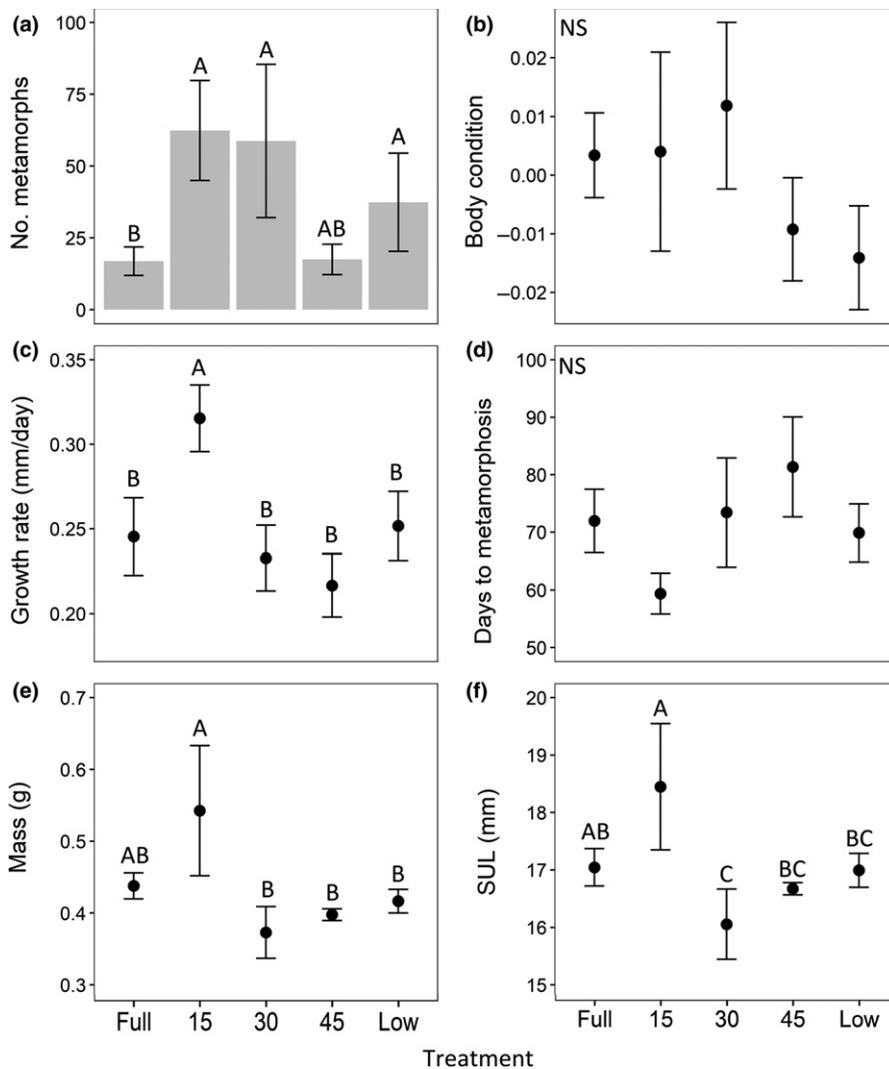
**TABLE 1** Mixed effects analysis results on metamorph survival, body condition, growth rate, length of the larval period, mass and snout-urostyle length

	df	$\chi^2$ or F	p
<b>Proportion metamorphs</b>			
Survival	1	32.96	<b>&lt;0.0001</b>
Treatment	4	15.60	<b>0.0036</b>
<b>Body condition</b>			
Survival	1	1.69	0.2034
Treatment	4	0.59	0.6752
<b>Growth rate</b>			
Survival	1	1.08	0.3053
Treatment	4	4.88	<b>0.0040</b>
<b>Larval period</b>			
Survival	1	4.96	<b>0.0325</b>
Treatment	4	1.84	0.1433
<b>Mass</b>			
Survival	1	8.73	<b>0.0056</b>
Treatment	4	3.50	<b>0.0189</b>
<b>Snout-urostyle length</b>			
Survival	1	11.88	<b>0.0015</b>
Treatment	4	4.15	<b>0.0091</b>

Notes. Test statistic is  $\chi^2$  for proportion of metamorphs, F for all others. Bold indicates statistical significance.

foci in ecology for much of its history (Clements, 1916; Connell, 1978; Hobbs & Huenneke, 1992; Pickett & White, 1985). In aquatic ecology, the dynamics of temporary ponds has been of particular interest and served as a model system in community ecology (e.g. Morin, 1981, 1983; Semlitsch et al., 1988; see reviews in Wellborn et al., 1996; Wilbur, 1997). With regard to animals, this work has focused on the role of the drying down of temporary ponds, with little consideration given to the effects of refilling or flooding, which can stop, delay or reverse the hydrologic and community dynamics. Annual and long-term successional changes are not always one-way processes (Amoros, Rostan, Pautou, & Bravard, 1987; Stringham, Krueger, & Shaver, 2003; Zweig & Kitchens, 2009). We investigated how refilling can affect the development of amphibians in small, soon to dry ponds. Filling did indeed alter the trajectory of larval *H. gratiosa* development, and the timing of filling within the larval period determined larval performance, likely due to the interaction of interconnected development stimuli and growth rate.

Responses to drying or refilling are likely driven by cues from two sources: environmental cues present from abiotic and biotic conditions within a habitat and conspecific cues related to intraspecific competition. However, competition is in part dependent on environmental conditions and the size and abundance of conspecifics. In our experiment, there were two levels of expected habitat quality: high (“full” mesocosms) or low (“low” mesocosms), and it is this component (habitat quality) that we directly manipulated via filling. We do not have measurements of physical and chemical



**FIGURE 2** Average (a) number of metamorphs and (b) body condition, (c) growth rate (length), (d) length of the larval period, (e) mass and (f) snout-urostyle length of metamorphs per mesocosm (means  $\pm$  SE). Treatments are arranged from left to right on a gradient of increasing amount of time spent at low water level. This corresponds to an environmental stress gradient from the minimum (“full” mesocosms) to maximum (“low” mesocosms) stress. “Full” mesocosms spent zero time at low water levels, “low” mesocosms the entire experiment at low water levels, and those refilled after 15, 30 and 45 days spent that number of days at low water levels. Body condition (b) is an index of length-specific mass. All figures are of raw data, and (a, d-f) had significant covariates that contribute to the displayed significance letters (see Table 1). NS indicates no significant differences

parameters in the water (temperature, dissolved solids, etc.) at any point in our experiment, and as such cannot directly assess differences between treatments. However, in small and drying ponds water parameters often vary in predictable ways, with more variable temperatures, less stratification, lower dissolved oxygen and higher dissolved solids (Burggren & Just, 1992; Matthews, 2010; Semlitsch, 1987; Williams, 2005). All of these factors can act as cues of habitat quality, cues that we would expect larvae in the four treatments that began at low volumes were exposed to, indicating a poor environment and initiating faster development. Conversely, larvae in our “full” mesocosms may not have been exposed to these same cues, or otherwise experienced differently than those in the treatments that began at depths of 15 cm. In turn, filling served to transition patches from risky to more stable habitats.

Intraspecific competition often negatively affects larval amphibian growth rates, although effects on size and length of the larval period are not always correlated and may vary independently due to various environmental cues (Collins, 1979; Travis, 1983a, 1984). At the start of the experiment, the small size of larvae (<5 mm), and their lower per capita food requirements, meant that there were

perhaps no significant competitive effects in any treatments. However, as time progressed and larvae grew, competition likely increased rapidly in mesocosms with low volumes. While this would increase the stimulus to grow and metamorphose sooner, eventually larval body sizes would be large enough that competition inhibited growth, yet larvae would be too small for metamorphosis to occur—resulting in mortality and/or stalled development. This is what we observed, with the highest mortality rates in the treatment (“low”) that spent the most time at low volume. While higher mortality in the “low” mesocosms and those filled after 45 days likely decreased competition, refilling after 45 days further decreased competition cues (e.g. larval density or food availability), providing less stimulus for metamorphosis in that treatment. Thus, despite similar overall survival rates, there was a trend towards more metamorphs from the “low” treatment than those filled after 45 days.

Filling earlier in development (mesocosms filled after 15 days) possibly alleviated competition-related stress, producing higher overall survival and more metamorphs than filling late in development (mesocosms filled after 45 days). We suspect that competitive stress was relatively low at the time of filling in mesocosms filled after

15 days, but that the faster development rates cued by initially risky conditions (small, shallow ponds) persisted even after filling. This meant that larvae in mesocosms filled after 15 days were on an accelerated developmental trajectory and had the fastest growth rates, while being under less competition than other treatments that remained at low volumes (fewer individuals per volume after filling), enabling them to reach metamorphosis at the largest size (Figure 3). Conversely, in mesocosms filled after 30 days, competition may have already slowed growth prior to filling but did not yet affect mortality. This produced similar overall survival and metamorphosis rates in these two treatments (filled after 15 and 30 days), but smaller individuals in mesocosms filled after 30 days than after 15 days. Individuals that survived to metamorphosis in the 45 and “low” treatments also had smaller body sizes, in combination with lower survival. *Hyla* larvae are generally herbivores that primarily feed on a variety of algae and are not cannibalistic (Altig, Whiles, & Taylor, 2007; Kupferberg, Marks, & Power, 1994), so cannibalism likely did not contribute to differences in survival among treatments.

“Full” mesocosms had high overall survival, yet produced as few metamorphs as mesocosms filled after 45 days, along with similarly small body sizes. “Full” mesocosms had the most surviving larvae at the end of the experiment, suggesting insufficient environmental or competitive stress to provide the cues for metamorphosis (Figure 3). Furthermore, all three filling treatments had very similar numbers of surviving larvae at the end of the experiment (albeit fewer than “full” and more than “low”; Appendix S1). This suggests that once mesocosms reached full depth, larvae on the trajectory to metamorphose did so. Other larvae were either too stunted to fully develop, or remained as larvae awaiting either a stimulus to metamorphose, or “elected” to obtain more resources, reach larger body sizes and wait for a future cue to initiate metamorphosis (sensu Wilbur & Collins, 1973). Temperature is perhaps the most critical abiotic factor affecting ectotherm development (Duellman & Trueb, 1986; Gillooly, Charnov, West, Savage, & Brown, 2002), and it is not surprising that production of metamorphs showed strong decreases after air temperatures began to decline in autumn, with the last metamorph emerging on 30 October. Across the duration of our experiment in 2014, ambient temperatures were not meaningfully different than

average: high temperatures in Oxford, Mississippi were on average 0.59°C below average, while low temperatures were 0.47°C below average. Remaining as larvae late into the season is a complete failure as a strategy, as there are no reports of *Hyla* larvae overwintering—all “surviving” larvae ultimately would have died before reaching metamorphosis. We ended our experiment in early November, as temperatures began to rapidly decline, and during our collections many larvae were lethargic in our mesocosms.

Traditional models of amphibian development state that lengthening of the larval period, under conditions of positive growth, is expected to benefit individual fitness by allowing individuals to reach larger sizes (Wilbur & Collins, 1973). Yet to be truly adaptive, longer larval periods also must enhance fitness (Newman, 1992; Tejedo & Reques, 1994), which does not occur if failure to metamorphose and mortality result. While our experiment was a simplified system designed for a novel test of the effects of filling small ponds on development, proximate stressors and cues are necessary to initiate metamorphosis (Denver, 1997a; Denver, Mirhadi, & Phillips, 1998). The conditions in our “full” mesocosms resulted in few metamorphs and many larvae that may have been waiting for the stimulus to metamorphose that never arrived. This is a fascinating paradox in the context of the Wilbur-Collins model and subsequent variations on that theme (Wilbur & Collins, 1973). What might explain this seemingly maladaptive behaviour? Across all treatments, the one set of cues clearly missing from our experiment are predator cues. In fishless ponds, predators tend to build up over time, so that anuran larvae experiencing low competition and low environmental stress would likely be experiencing some perceived predation pressure that could provide the cue for metamorphosis (sensu Werner & Gilliam, 1984). However, when mesocosms were at full volumes, several factors that can act as cues to initiate metamorphosis such as water temperature, dissolved solids and conspecific densities were likely reduced, resulting in more larvae that did not metamorphose. Selection can only work on scenarios to which organisms are exposed; the predation-free, low competition, low environmental stress environment that was likely experienced in our “full” mesocosms may simply occur at such a low frequency under natural conditions that it is inaccessible to selection. Our “full” mesocosms may simply have been too benign of a control to effectively stimulate metamorphosis in an experimental system.

Although we have limited evidence from a single amphibian species, we can begin to question the efficacy of some traditional management or restoration strategies aimed at improving habitat for amphibians or other organisms with complex lifecycles adapted to temporary ponds (Knapp, Boiano, & Vredenburg, 2007; Walston & Mullin, 2007). While fish removal has been a dominant paradigm for habitat improvement in freshwater systems (Moss, 1990; Søndergaard, Liboriussen, Pedersen, & Jeppesen, 2008), it may not be the most effective amphibian restoration strategy, as fish almost universally occupy permanent ponds. Given the poor *H. gratiosa* productivity we observed in our “full” mesocosms, making permanent ponds fishless may not be the most effective method for restoring amphibian populations, and may be better coupled with the establishment

	Full	15	30	45	Low
Survival	↑	↑	↑	↓	↓
Metamorphs	↓	↑	↑	↓	↑
Body condition	↑	↑	↑	↓	↓
Growth rate	↓	↑	↓	↓	↓
Larval period	↑	↓	↑	↑	↑
Length	↓	↑	↓	↓	↓
Mass	↓	↑	↓	↓	↓

**FIGURE 3** Representation of how filling mesocosms affects the development of *H. gratiosa* across all of the five treatments and all variables. Green indicates the direction of change is beneficial, red indicates detrimental changes. Up arrows indicate an increase in that measure, down arrows a decrease [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

of a drying regime, or rather the creation of new temporary ponds. Natural temporary ponds containing a diverse community of organisms, including non-fish predators such as salamanders and predatory insects, can provide habitats for amphibians that not only enable them to reach metamorphosis, but also provide adequate stimuli that push them to do so.

Human alteration of natural landscapes has changed hydroperiod and natural flow regimes of lentic and lotic systems (Cloern, 2007; Gore & Shields, 1995; Poff et al., 1997). At the same time, alteration of terrestrial landscapes through urbanisation and deforestation has increased the frequency and magnitude of floods, as well as variability of hydroperiods, with large pulses that refill lentic habitats (Hollis, 1975; Klein, 1979; Nirupama & Simonovic, 2007). The intermittency of many lentic habitats was historically driven by fairly predictable seasonal patterns of precipitation and evapotranspiration (Brooks, 2000; Williams, 1996), but as climate change progresses hydrologic regimes will certainly change (Booij, 2005; Christensen & Christensen, 2003). Thus, studying the potential effects of these changes is critical for understanding how species respond in a changing world.

The duration of ephemeral habitats and the occurrence of disturbances are clearly among the most important drivers of community structure and individual development in many systems. Physical stress is often the primary regulator of biotic changes associated with disturbance and deteriorating habitats, whereas competitive effects may become more dominant in longer duration, less disturbed habitats (Lubchenco, 1986; Wilbur, 1987). As ponds dry abiotic characteristics change at the same time as species interactions do, resulting in potential interactions between abiotic and biotic characteristics of ponds (Pintar & Resetarits, 2018b,c Semlitsch & Wilbur, 1988). In permanent habitats, predators are more abundant and regulate prey populations and community structure (Schneider & Frost, 1996; Wilbur, 1997). Traditionally, research has focused on the deterioration of habitats and disturbances that have negative effects on individual development. We observed that a positive change to a risky habitat can not only affect larval anuran development, but also that its effects are dependent on when they occur in larval development. Such habitat changes could have significant implications for frog populations. The duration and disturbance of habitats mediate the interconnected effects of predation, competition and environmental stress in natural systems, generating the patterns of biodiversity and community structure that we observe.

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## CONFLICT OF INTEREST

The authors declare no conflicts of interest.

## AUTHORS' CONTRIBUTIONS

MRP conceived, designed and conducted the experiment. MRP analysed the data and wrote the manuscript with input from WJR.

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## SUPPORTING INFORMATION

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