



Filling ephemeral ponds affects development and phenotypic expression in *Ambystoma talpoideum*

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Abstract

1. Populations and communities are often greatly affected by disturbances and variation in abiotic habitat conditions. Many of these effects are contingent on relatively predictable, yet still variable, environmental conditions that drive the life history strategies and development pathways of organisms in those habitats. However, much focus has been placed on aspects of such changes that cause mortality or movement from patches, whereas a multitude of outcomes can occur in natural systems. In lentic freshwater habitats, hydroperiod is a defining environmental characteristic, with temporary ponds supporting distinct communities of organisms with complex life cycles and plastic developmental trajectories.
2. Little consideration has been given to the effects of refilling of ponds with variable hydroperiods, as lengthening the hydroperiod can extend the time organisms spend in their aquatic stages, allowing for the acquisition of more resources. We hypothesised that increasing the volume of small ponds and adding competitors (*Ambystoma maculatum*) at the time of filling would interactively affect the development and phenotypic expression of *Ambystoma talpoideum*.
3. We introduced larval *A. talpoideum* to experimental mesocosms and manipulated water level (small, low volume mesocosms; filled, full mesocosms) and the addition of competitors (*A. maculatum*) at the time of filling in a 2 × 2 factorial design.
4. We found that low volume mesocosms were dominated by metamorphs, while filling resulted in a more even mix of metamorphs, larvae and paedomorphs in full mesocosms. Filling resulted in larger metamorphs and paedomorphs, but did not affect larvae, whereas addition of *A. maculatum* shortened the larval period of metamorphs.
5. We provide evidence that changes in abiotic habitat conditions, such as variation in the volume of ponds, can shift the development and phenotype of organisms. This plasticity may allow species to ensure the success of populations under both improvement and deterioration of environmental conditions. Hence, phenotypes like paedomorphic *A. talpoideum* can breed sooner than metamorphs, theoretically maximising the fitness of both individuals and populations.

KEYWORDS

life history trade-off, paedomorphosis, phenotype, polyphenism, temporary ponds

1 | INTRODUCTION

Landscapes are heterogeneous mosaics of habitat patches that result in a myriad of characteristics. Habitat duration and disturbance frequency are dominant drivers of population structure, individual fitness and community composition in many systems (Chesson, 2000; Hobbs & Huenneke, 1992; Schneider, 1997; Sousa, 1984). Changing habitat quality can have direct and indirect effects via both abiotic and biotic components that have lethal and non-lethal effects on resident organisms, altering interactions and shifting the competitive balance among interacting species (Chalcraft & Andrews, 1999; Rogers & Chalcraft, 2008; Sousa, 1984; Wootten, 1994). Changes in habitat characteristics and actual and/or perceived quality can affect fitness and shape population and community structure through changing cues that drive critical life history decisions and can initiate movement from patches (Denver, 1997; Newman, 1987; Pfennig, 1990; Skúlason & Smith, 1995).

In heterogeneous environments, many organisms have complex life cycles and developmental plasticity that allow individuals and/or populations to persist through variable conditions. Life history events are often timed to match or are cued by temporal changes in habitat conditions, such as the breeding of anuran amphibians in ponds soon after they fill and metamorphosis prior to drying (Denver, 1997; Pintar & Resetarits, 2017; Wilbur, 1980). Some organisms with plastic life histories living in variable environments manifest their responses to heterogeneity through polyphenisms—individuals of the same age and genotype can express different phenotypes depending on the conditions experienced (Bradshaw, 1965; Relyea, 2001; Sibly, 1995). This adaptive phenotypic plasticity occurs when the phenotype conferring the highest relative fitness varies with environmental conditions (Brady & Griffiths, 2012; Gotthard & Nylin, 1995; Stearns, 1989; Thompson, 1991). Phenotypic expression can be driven by both abiotic and biotic conditions, but often the two are linked, as abiotic changes such as shifts in physical habitat structure initiate many biotic changes (Anderson, Mott, Levine, & Whiteman, 2013; Semlitsch, 1987b; Wellborn, Skelly, & Werner, 1996). Phenotypic traits can be discrete or continuous, and there is typically a high correlation between the degree of phenotypic plasticity and environmental heterogeneity (Lind & Johansson, 2007; Via & Lande, 1985). In highly variable systems, such as temporary ponds, phenotypic plasticity is critical as it fine-tunes the complex life cycles of the insects, amphibians and other taxa that occupy these habitats at one life stage and switch habitats for other life stages (Moran, 1992; Rowe & Ludwig, 1991; West-Eberhard, 1989).

Abiotic changes that occur in habitats as they progress through seasonal or temporal habitat duration cycles play critical roles in shaping biotic changes, and this is particularly true in freshwater systems, where habitat duration is determined by the amount of time habitat patches retain water. The transition from permanent to temporary is a defining characteristic of freshwater habitats that shapes community structure (Wellborn et al., 1996). In particular, the presence and identity of predators varies along this hydroperiod gradient

with fish as the dominant predators in permanent ponds and invertebrates and larval amphibians the dominant predators in temporary and permanent fishless ponds (Batzer & Wissinger, 1996; Stoks & McPeck, 2003; Wellborn et al., 1996; Wissinger, Whiteman, Sparks, Rouse, & Brown, 1999). Organisms inhabiting ephemeral habitats, and temporary ponds in particular, should have higher developmental plasticity than those only found in permanent habitats where cues are novel or variable in their timing (Wilbur & Collins, 1973). Developmental effects have been well studied in drying ponds: as hydroperiod decreases, metamorphosis of insects and amphibians occurs earlier and at smaller body sizes (Juliano & Stoffregen, 1994; 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 can allow individuals to avoid desiccation, the resulting smaller body sizes can affect future fitness, since larger individuals have better overwinter survival, higher breeding success and produce more offspring (Berven, 1981; Berven & Gill, 1983; Semlitsch, Scott, & Pechmann, 1988; Smith, 1987).

Habitat duration and associated abiotic changes in habitats are often viewed as being dependent on relatively predictable environmental conditions. This leads to a somewhat deterministic perspective on habitat duration, in which once a habitat begins moving towards the end of its existing state, it completes that cycle (Newman, 1988; Schneider & Frost, 1996). However, this is not necessarily representative of the range of outcomes in natural systems, as the hydroperiod of drying freshwater habitats can be extended through refilling, potentially shifting the development of resident organisms. This is a particularly important consideration since, as climate change progresses, not only will typical weather regimes change, but also extreme events are predicted to become more common, potentially resulting in both larger precipitation events and more severe droughts (Houghton et al., 1995; Katz, 2010).

In lentic freshwater systems, pond drying is not always a one-way process; precipitation or flooding can refill ponds at any time, not only after a pond has completely dried. Refilling can increase pond volume and surface area, reducing conspecific density, and also import nutrients and other resources that can support higher productivity (Thomaz, Bini, & Bozelli, 2007). When dry areas within pond basins are submerged, short periods of accelerated biogeochemical reactions and biological processes result (McClain et al., 2003; McKnight et al., 1999; Stanley, Fisher, & Jones, 2004). Conversely, aquatic and semiaquatic plant communities are adapted to specific hydrologic regimes, and filling or drying that diverges from this regime can negatively affect plant survival, propagation and germination (Coops & Van der Velde, 1995; Poiani & Johnson, 1989). At the same time, flooding can enable the immigration of competitors and predators from surrounding habitats. Many of these organisms—predatory fish in particular—can have drastic effects by consuming the denizens of temporary ponds (Hartel et al., 2007; Hecnar & M'Closkey, 1997; Teplitsky, Plénet, & Joly, 2003).

Because many animals inhabiting temporary ponds already have the plasticity to respond to changing environmental conditions, and pond drying in particular, we would expect them to also have the ability to shift their developmental trajectory in response to filling ponds. If change in abiotic habitat characteristics coincides with the introduction of organisms to a habitat, we might expect these abiotic and biotic changes to interactively impact resident organisms. Our goal was to assess the effects of refilling ponds and the addition of competitors (*Ambystoma maculatum*) during refilling on the survival, morphotype and development of *Ambystoma talpoideum*. This was done to simulate a large rainfall event or flood that fills a small, soon to dry pond and introduces additional competitors to that pond from nearby ponds. We hypothesised that refilling ponds would increase survival, body size and the proportion of larvae and pedomorphs, while adding *A. maculatum* would not affect survival, decrease body size and shift *A. talpoideum* morph production away from pedomorphs.

2 | METHODS

2.1 | Study species

Our focal species, the mole salamander, *Ambystoma talpoideum*, is a common inhabitant of ponds and widely distributed across the south-eastern United States. It is facultatively pedomorphic, exhibiting two ontogenetic morphs: metamorphs that fully metamorphose and become sexually mature terrestrial adults, and pedomorphs that are aquatic, sexually mature individuals that retain larval morphology. Pedomorphosis can occur under advantageous or certain disadvantageous conditions, but in small ponds that have high chance of drying, we would expect pedomorphosis to be rare (Semlitsch & Wilbur, 1988; Whiteman, 1994). Ponds may also contain immature aquatic larvae that have not initiated a pathway to maturation. Various environmental stimuli drive the expression of each morph, which are maintained in a population through fitness trade-offs and environmental variability (Doyle & Whiteman, 2008; Jackson & Semlitsch, 1993; Semlitsch, 1985, 1987b; Semlitsch & Wilbur, 1988). Larval *Ambystoma maculatum*, the spotted salamander, commonly co-occur in ponds with *A. talpoideum*, but exhibit obligate metamorphosis and rarely overwinter as larvae (Whitford & Vinegar, 1966). The two species have differences in competitive abilities, with *A. talpoideum* being a dominant interference competitor and *A. maculatum* a dominant exploitative competitor (Walls, 1996; Walls & Jaeger, 1987). Furthermore, the larval period of *A. maculatum* is typically much shorter than that of *A. talpoideum*, with *A. maculatum* metamorphosing by midsummer in the south-eastern United States (Petranka, 1998). This differential competitive ability, combined with the relatively short duration of co-occurrence of the two species in ponds, allowed us to test for interactive effects between refilling ponds and adding competitors on the morphotype expression and body size of *A. talpoideum*.

2.2 | Experimental design

Our experiment was conducted at the University of Mississippi Field Station (UMFS) in north-central Mississippi, USA. On 17 January 2015, mesocosms (plastic cattle tanks: 1.8 m diameter, ~1,300 L (maximum), $n = 29$) were filled to a depth of 17 cm (approximately one-third of the maximum depth of 52 cm) with water from a nearby pond that was filtered through 1.13×1.3 -mm fibreglass mesh. Adjustable standpipes were attached to mesocosms to maintain desired water levels. We randomly added 3 kg of dry hardwood leaf litter (primarily *Platanus occidentalis*) to each mesocosm as a nutrient base to support primary and secondary productivity.

Ambystoma maculatum egg masses were collected from ponds at UMFS on 18 January and placed in holding pools where they hatched and remained until April. *Ambystoma talpoideum* egg masses were obtained by collecting pairs of metamorphic adults at UMFS and placing them in holding pools where they laid eggs on 13 January. Adults were sourced from ponds that are known to dry annually and situated among mixed forest habitat along headwater streams. These eggs were transferred to the laboratory until they hatched. Using seven separate clutches, we assembled aggregate groups of 15 larvae, with two larvae sourced from each clutch plus one randomly selected individual. These groups of 15 *A. talpoideum* larvae were randomly assigned and added to each mesocosm immediately after they hatched on 28 January.

In our 2×2 factorial design, filling (water level: "low" [no water added], "full" [filled to maximum volume]) was crossed with the addition/non-addition of five *A. maculatum* larvae after completion of filling on 21 April. Treatment was randomly assigned within blocks (spatial positioning within the array, rows of mesocosms south to north from a treeline). On 21 April, mesocosms assigned to our "full" treatment were filled with water pumped from the same source pond in the same manner as initial filling. Mesocosms were completely filled from initial depths of 17 cm to final depths of 52 cm in approximately 10 min, representing a single, large filling event, such as those that we have observed at UMFS during large precipitation events (approximately >25 mm rainfall per day). On 22 April, five *A. maculatum* larvae were added to each mesocosm in the treatments assigned to receive additional salamanders.

A fifth treatment (10 added *A. maculatum* to "full" mesocosms) did not materialise due to limited *A. maculatum* availability, which was not realised until after filling mesocosms on 21 April. We added these mesocosms into other treatments in our 2×2 design. This, along with a structural failure of one mesocosm, resulted in an unbalanced design. Final replication of each treatment was as follows: six "low" mesocosms that did not receive *A. maculatum*, six "low" mesocosms that received *A. maculatum*, eight "full" mesocosms that did not receive *A. maculatum* and nine "full" mesocosms that received *A. maculatum* (overall $n = 29$).

We checked mesocosms every other night from mid-May through August, every third night in September and October, and

every morning May through November for metamorphs. Metamorphs were collected, massed, photographed and released near source ponds at UMFS. Metamorphs were dorsally photographed in standardised positions with scales for calibration in ImageJ (Schneider, Rasband, & Eliceiri, 2012), which we used to measure snout-vent length (SVL) and head width. We estimated SVL from dorsal photographs as the point immediately posterior to the legs. The experiment was terminated on 24 November 2015, when we deconstructed the experiment and collected all remaining individuals. The remaining individuals were processed in the same manner as metamorphs, and their morphotype (immature larva, paedomorph) was determined by visually inspecting for enlarged eggs in females and swollen cloacal glands in males, which are indicative of sexually mature paedomorphs (Scott, 1993).

2.3 | Data analysis

We used type III sums of squares, $\alpha = 0.05$, and all analyses were conducted in R v.3.4.1 using the car package v.2.1-5 and lme4 package v.1.1-13 (Bates, Mächler, Bolker, & Walker, 2015; Fox & Weisberg, 2011; R Core Team, 2017). Count data were square root-transformed ($\sqrt{X+0.5}$), and body measurements were log-transformed.

2.4 | Survival and morphotype

We determined the effect on survival/mortality using logistic regression with water level, *A. maculatum* addition, and their interaction as fixed effects. Among surviving individuals (excluding mortality), the proportions of individuals expressing each morphotype (immature larvae, metamorphs, paedomorphs) were analysed using logistic regression with water level, *A. maculatum* addition, and their interaction as fixed effects and overall survival as a covariate. The effect of water level on *A. maculatum* survival was also analysed with logistic regression. All logistic regressions were conducted with the glmer function in the lme4 package (Bates et al., 2015) and used a binomial error distribution and mesocosm nested within treatment as random effects to correct for overdispersion, as the residual deviances were large relative to the residual degrees of freedom (Warton & Hui, 2011).

2.5 | Individual measures

All individual analyses included survival, water level, *A. maculatum* addition and the water level \times *A. maculatum* addition interaction as fixed effects and block as a random effect in mixed-effects models that were analysed using restricted maximum-likelihood *F* tests due to unbalanced designs. These analyses utilised the lmer function in the lme4 package and the lmerTest package for Satterthwaite approximation of the degrees of freedom (Bates et al., 2015; Kuznetsova, Brockhoff, & Christensen, 2017). Survival was included as a covariate because higher survival would be expected to increase competition and decrease growth (Semlitsch, 1987a). Overall survival

(metamorphs + larvae + paedomorphs) was the covariate in metamorph analyses, whereas final number of individuals in each mesocosm (larvae + paedomorphs) was the covariate in larval and paedomorph analyses as it is more representative of the conditions these two morphs experienced at the end of the experiment when their measurements were taken. Including length of the larval period as a covariate in metamorph analyses did not significantly affect results ($p > 0.5$), so we excluded it from our models. Each morph was analysed separately using averages of all individuals of that morphotype in each mesocosm to avoid pseudoreplication.

For each of the three morphotypes, we independently analysed averages of three body size measures (mass, SVL and head width). These three measures were independently analysed because we did not necessarily expect correlative responses among them. Enlarged relative head width can be an indication of feeding ability and cannibalism in salamanders (Kohmatsu, Nakano, & Yamamura, 2001), so we included SVL as a fixed covariate in that analysis. Mass can be an indication of food availability, which we explored further with the body condition analysis. We calculated and analysed body condition (size independent mass) by mean-scaling mass to decouple variance from the measurement scale and means, regressing against SVL and using the residuals in a mixed-effects model (Berner, 2011). We conducted two additional analyses on metamorphs only: length of the larval period (days to metamorphosis) and growth rate (mm of SVL per day). Growth rate for larvae and paedomorphs was not analysed as it would be a proportional linear transformation of SVL.

3 | RESULTS

3.1 | Survival and morphotype

Ambystoma maculatum metamorphs emerged from 12 May through 12 July, and *A. talpoideum* metamorphs emerged from 2 June through 1 November. There were no *A. maculatum* larvae remaining in mesocosms at the end of the experiment, and none were observed after the last metamorph on 12 July. *Ambystoma talpoideum* survival was not affected by water level ($\chi^2_1 = 0.40$, $p = 0.5286$), *A. maculatum* addition ($\chi^2_1 = 0.00$, $p = 0.9469$) or their interaction ($\chi^2_1 = 0.15$, $p = 0.6963$) (Figure 1). The proportion of metamorphs was affected by water level, with a marginal water level \times *A. maculatum* addition interaction (Table 1; Figure 2a). The proportion of larvae positively covaried with survival, and there was a significant water level \times *A. maculatum* addition interaction (Figure 2b). The proportion of paedomorphs negatively covaried with survival and was affected by water level, but there was no interaction (Figure 2c). Overall, there were more metamorphs from all four treatments than any other morphotype, with the most metamorphs in "low" mesocosms that did not have *A. maculatum* added. "Low" mesocosms that had *A. maculatum* added, and "full" mesocosms that did not, had the most immature larvae at the end of the experiment, whereas "low" mesocosms without *A. maculatum* had the fewest larvae. "Full" mesocosms with *A. maculatum* added had the most paedomorphs, whereas "low" mesocosms without *A. maculatum* had the

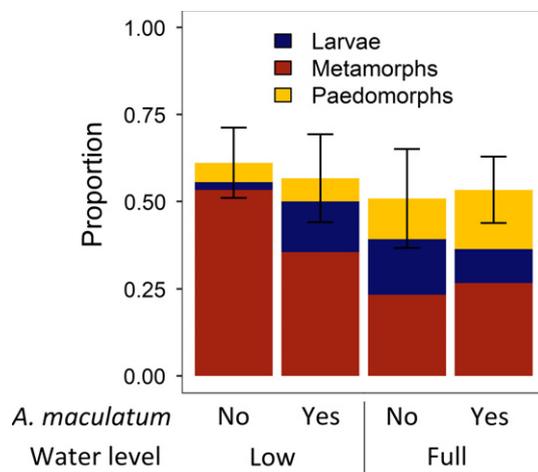


FIGURE 1 The average overall proportion of individuals surviving per mesocosm (larvae + metamorphs + paedomorphs) from each treatment (means \pm SE). Bars are divided into the proportion represented by each of the three morphotypes. See Figure 2a–c for numbers of individuals representing each morph [Colour figure can be viewed at wileyonlinelibrary.com]

fewest paedomorphs. Water level had no effect on *A. maculatum* survival ($\chi^2_1 = 1.73$, $p = 0.188$).

3.2 | Individual measures

Water level had significant main effects in several analyses (Table 1; Figure 2). Mass of both metamorphs and paedomorphs, but not larvae, was significantly greater among individuals in “full” mesocosms than in “low” (Figure 2d–f), and the larval period of metamorphs was significantly longer in “full” mesocosms than in “low” (Figure 3a). There were significant main effects of *A. maculatum* addition in only two analyses (Table 1): metamorph growth rate was slower (Figure 3b) and metamorph larval period longer (Figure 3a) in mesocosms that received *A. maculatum* than those that did not (Figure 2n).

Survival was a significant covariate in mass and SVL analyses for all three morphs, paedomorph head width, and in analyses of larval body condition, and metamorph growth rate and larval period (Table 1). Among all morphs, higher survival resulted in smaller body sizes, whereas in metamorphs, the length of the larval period was longer when survival was higher (Figure 4a). The water level \times *A. maculatum* addition interaction was significant in only the paedomorph body condition analysis (Figure 2o). Head width positively covaried with SVL among metamorphs and paedomorphs, but not among larvae. Head width did not vary with water level, *A. maculatum* addition, or their interaction among larvae and paedomorphs, but was affected by water level among metamorphs (Figure 2g–i); relative metamorph head width was larger in “full” mesocosms than in “low.” Paedomorph body condition was higher in “full” mesocosms that did not receive *A. maculatum* than in mesocosms that did, but “low” mesocosms again did not differ (Figure 2o).

Replication of treatments for larval body measures was low overall (Figure 2e), with only one replicate “low” mesocosm that did not

receive *A. maculatum* included. Low replication may have resulted in a loss of power for some treatments/morphs. This level of replication was dependent on the developmental trajectories of individuals within each mesocosm, so it is not something we could knowingly account for a priori and may have contributed to differences in responses among larvae relative to metamorphs and paedomorphs (Figure 2).

4 | DISCUSSION

Changing conditions within a habitat patch can have both beneficial and detrimental effects on resident organisms by affecting their survival, growth and development. By filling ponds with low volumes, we were able to test for effects on the development and population structure of *A. talpoideum* under conditions where lentic freshwater habitats rapidly transit from poor- to high-quality habitat patches during the larval stage. Overall, filling mesocosms shifted morphotype expression in each mesocosm and enabled individuals to reach larger sizes, regardless of morph, whereas addition of *A. maculatum* had effects that were largely limited to length of metamorph larval period (Figure 5). This indicates that *A. talpoideum* were able to take advantage of improving environmental conditions in their aquatic habitats, and that competitive effects of *A. maculatum* were mostly transient, as they completed metamorphosis by midsummer. The developmental plasticity of *A. talpoideum* enabled them to assume the phenotype that would be expected to maximise fitness, given the environmental conditions they experienced. Their perception of environmental conditions would be based on cues of habitat duration and intraspecific and interspecific competition in our experiment (Semlitsch et al., 1988).

Survival had large effects in most of our analyses of individual variables (Table 1), and intraspecific competition is known to affect size of *A. talpoideum* and other amphibians (Burraco, Díaz-Paniagua, & Gomez-Mestre, 2017; Semlitsch, 1987a,b). Thus, it is not surprising that survival, which we used as an indicator of intraspecific competition, had such large effects in our experiment. While our treatments had no main effects on survival in our analyses, the number of survivors in each mesocosm still varied considerably—as low as 0 per cent and as high as 100 per cent. Body sizes were predictably larger when survival was lower (Figure 4a), meaning that lower competition likely enabled individuals to obtain more resources.

We observed effects of water level on specific body size measures after removing effects of survival. Mesocosms with low volumes had metamorphs and paedomorphs with smaller mass, but SVL of all morphotypes and final larval measurements were unaffected. Larger relative head widths among metamorphs in “full” mesocosms could be a response to potentially higher resource availability after filling, which also enabled them to reach larger masses. During the aquatic stages, larger individuals are more likely to become paedomorphic than remain as larvae (Semlitsch, 1987a). This could potentially explain some of the lack of effects of filling mesocosms on

TABLE 1 Analysis results. Tests statistics are chi-square for morph proportions and *F* for all other measures. Bold indicates statistical significance

	df	Metamorphs		Larvae		Paedomorphs	
		χ^2 or <i>F</i>	<i>p</i>	χ^2 or <i>F</i>	<i>p</i>	χ^2 or <i>F</i>	<i>p</i>
Morph proportion							
Survival	1	0.24	0.6255	6.15	0.0131	9.62	0.0019
Water level	1	9.58	0.0020	1.67	0.1960	7.43	0.0064
<i>A. maculatum</i>	1	2.02	0.1556	2.46	0.1170	0.22	0.6377
Water level: <i>A. maculatum</i>	1	3.00	0.0833	5.64	0.0175	0.01	0.9352
Mass							
Survival	1	39.67	< 0.0001	10.81	0.0111	53.84	< 0.0001
Water level	1	4.63	0.0439	0.06	0.8072	5.62	0.0316
<i>A. maculatum</i>	1	2.63	0.1202	0.22	0.6526	0.51	0.4848
Water level: <i>A. maculatum</i>	1	0.60	0.4471	1.55	0.2488	0.07	0.7939
Head width							
Survival	1	0.85	0.3670	0.41	0.5402	5.50	0.0343
Snout-vent length	1	91.94	< 0.0001	2.98	0.1281	10.69	0.0056
Water level	1	5.05	0.0367	0.89	0.3779	1.84	0.1967
<i>A. maculatum</i>	1	3.82	0.0654	0.66	0.4426	0.09	0.7701
Water level: <i>A. maculatum</i>	1	0.47	0.5008	0.44	0.5281	1.18	0.2953
Snout-vent length							
Survival	1	51.41	< 0.0001	14.68	0.0050	31.95	< 0.0001
Water level	1	1.91	0.1819	0.08	0.7874	1.87	0.1918
<i>A. maculatum</i>	1	1.01	0.3278	0.02	0.8870	0.47	0.5045
Water level: <i>A. maculatum</i>	1	0.50	0.4893	0.21	0.6553	0.74	0.4046
Body condition							
Survival	1	0.07	0.8011	7.49	0.0313	0.14	0.7123
Water level	1	1.02	0.3245	1.05	0.3413	0.12	0.7342
<i>A. maculatum</i>	1	0.03	0.8768	3.97	0.0934	0.48	0.4994
Water level: <i>A. maculatum</i>	1	0.06	0.8028	4.18	0.0813	5.47	0.0350
Larval period							
Survival	1	12.57	0.0020				
Water level	1	4.11	0.0561				
<i>A. maculatum</i>	1	9.01	0.0070				
Water level: <i>A. maculatum</i>	1	0.14	0.7131				
Growth rate (SVL/day)							
Survival	1	44.31	< 0.0001				
Water level	1	0.71	0.4110				
<i>A. maculatum</i>	1	5.22	0.0335				
Water level: <i>A. maculatum</i>	1	0.05	0.8306				

larval and paedomorphic body size measures, as effects of size manifested themselves not as variation in size within a morph, but in differences in morphotype expression from each treatment.

Filling mesocosms shifted morphotype expression in each treatment from metamorph-dominated in "low" mesocosms to a more even distribution of the three morphs in "full" mesocosms (Figure 1). These results suggest that filling mesocosms improved the conditions in those habitats, affecting *A. talpoideum* development. Filling

mesocosms could have reduced conspecific density (individuals/volume), increased food availability, decreased competition or affected other habitat characteristics that *A. talpoideum* responded positively to. Intraspecific competition is an important component of *A. talpoideum* growth and development (Semlitsch, 1987a,b), and when there is more even distribution of morphs (independent of pond volume), per capita competition can effectively be reduced by distributing individuals among both aquatic and terrestrial habitats,

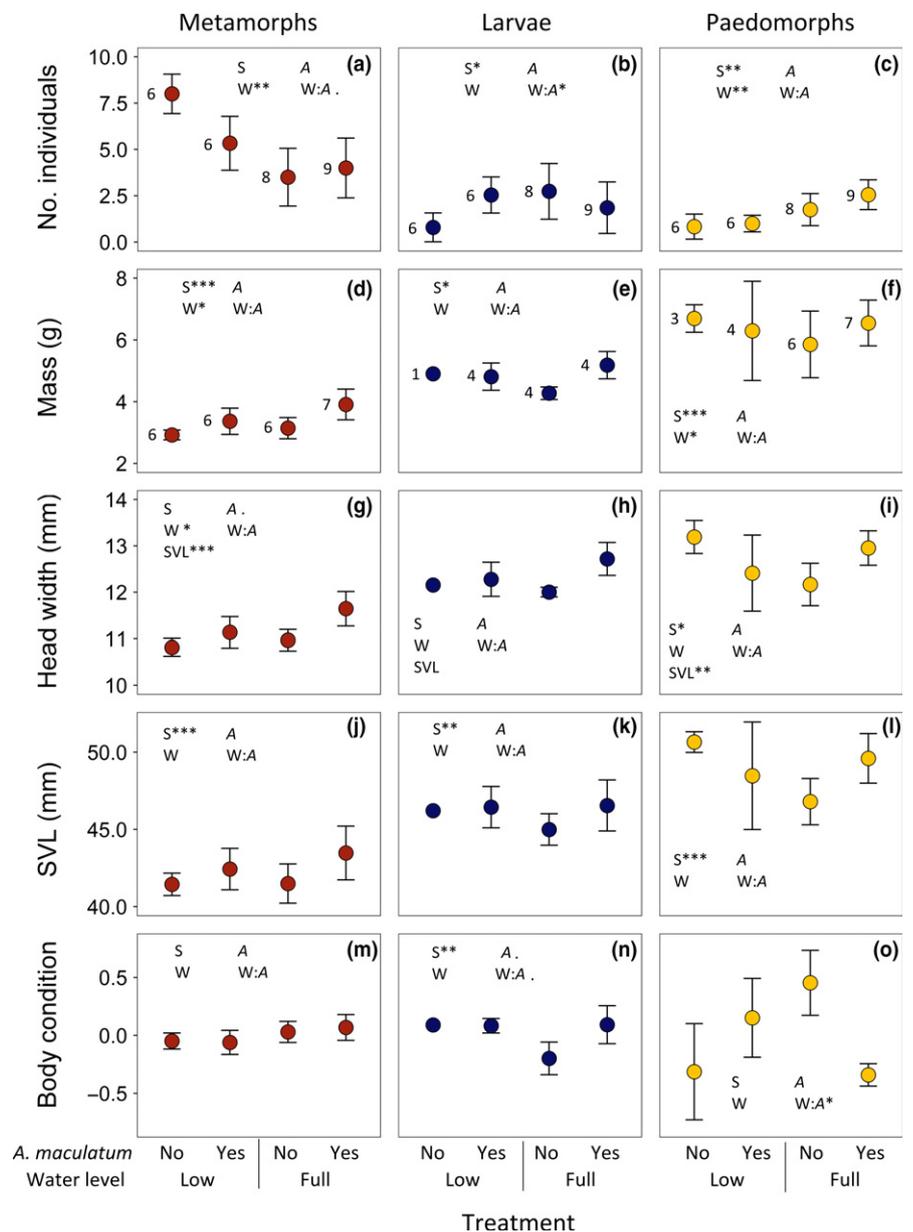


FIGURE 2 Average (a–c) number of individuals, (d–f) mass, (g–i) head width, (j–l) snout-vent length (SVL) and (m–o) body condition of individuals per mesocosm from each morphotype and treatment (means \pm SE). S = survival; W = water level; A = *A. maculatum*; W:A = water level \times *A. maculatum* interaction; SVL = snout-vent length. Significance of these effects are indicated by *** p < 0.001; ** p < 0.01; * p < 0.05; p < 0.10. If none of those symbols are present, p > 0.10 (see Table 1 for full results). Body condition (m–o) displays the residuals from the analysis on the y-axis (see Materials and Methods). Numbers in (a–c) indicate number of overall replicate mesocosms of that treatment. Numbers in (d–f) indicate the number of replicate mesocosms producing individuals of that morphotype (sample size); these numbers are also applicable to (g–o), for each respective morph [Colour figure can be viewed at wileyonlinelibrary.com]

rather than predominantly one habitat as was the case with metamorphs in our “low” mesocosms. If there is a cost to maintain plasticity, and *A. talpoideum* were consistently exposed to habitats that produced mostly metamorphs, selection could act to reduce or eliminate the plasticity that enables the persistence of the three morphs. However, variable environments present a multitude of scenarios to *A. talpoideum* across different habitat patches, so selection has clearly favoured phenotypic plasticity. Because *A. talpoideum* responded to filling with greater variation in morph expression, this supports the idea that their developmental strategy is not fixed early in the larval stage, but is dependent on conditions later in development, as well as the interaction between conditions early and late in development (Ryan & Semlitsch, 2003).

Addition of *A. maculatum* shortened the larval period of metamorphs, but did not affect size at metamorphosis, resulting in growth rates of metamorphosed *A. talpoideum* larvae that were higher when

A. maculatum were present. We added five *A. maculatum* to each mesocosm, compared to 15 *A. talpoideum*, so it is possible that interspecific competition was too low to have an effect on metamorph size. However, the presence of *A. maculatum* added cues that indicated higher total abundances of competitors, which could result in faster development with or without affecting body sizes. In natural systems, including many of the ponds at UMFS, both species simultaneously occupy the same ponds for much of their larval period, until *A. maculatum* metamorphose in summer. During this time, competition among larvae of both species is often high, so earlier metamorphosis can benefit individuals by moving into terrestrial habitats where they are able to continue growth and development while escaping the often high competition and potential desiccation risk of aquatic habitats. We observed no effects of *A. maculatum* on larvae or paedomorphs, as their measurements were taken about 4.5 months after the last *A. maculatum* metamorphosed—likely enough

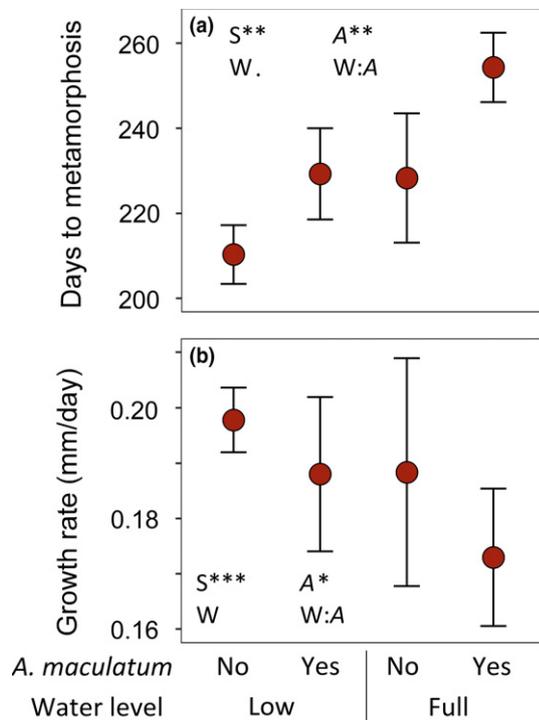


FIGURE 3 Average (a) length of the larval period and (b) growth rate (mm of SVL per day) of metamorphs per mesocosm from each treatment (means \pm SE). Letters and symbols are the same as Figure 2, and replication is the same as Figure 2d [Colour figure can be viewed at wileyonlinelibrary.com]

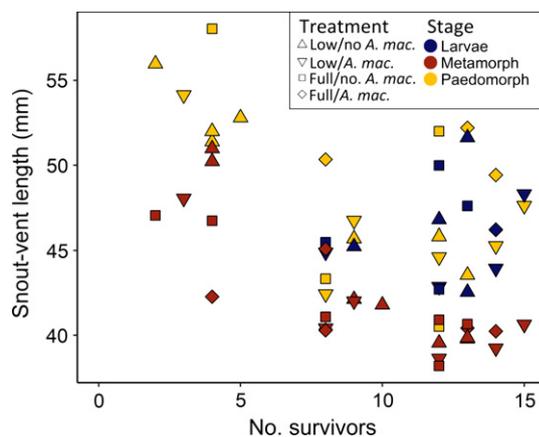


FIGURE 4 Average snout-vent length of individuals from each morph and mesocosm versus number of total survivors from that mesocosm (metamorphs + larvae + paedomorphs; 15 = 100% survival) [Colour figure can be viewed at wileyonlinelibrary.com]

time to allow compensation for effects earlier in development. *Ambystoma maculatum* addition may have affected metamorphs because many individuals that metamorphosed did so in summer and thus had a larger proportion of their aquatic phase in the presence of *A. maculatum* than either paedomorphs or overwintering larvae. Why we observed significant interactions between *A. maculatum* addition and water level in the paedomorph body condition analysis, but not other analyses, is puzzling and lacks adequate explanation.

From prior work, hydroperiod and drying down of ponds clearly affect both morphotype expression and development of *A. talpoideum*, among other amphibians (Brady & Griffiths, 2012; Denver, Mirhadi, & Phillips, 1998; Semlitsch, 1987b; Semlitsch & Wilbur, 1988). Metamorphosis is dominant in drying ponds, but while none of our mesocosms ever actually dried, we observed larger proportions of metamorphs in “low” mesocosms. By the end of the experiment, the low numbers of *A. talpoideum* remaining in “low” mesocosms suggested that reduced intraspecific competition allowed some individuals to become paedomorphic and others to remain as larvae. However, we still observed more metamorphs from “full” mesocosms than either of the other two morphotypes. Studies of the effects of hydroperiod have shown that starting and remaining at favourable conditions (i.e. in a “full” mesocosm throughout the experiment) will produce predominantly paedomorphs (Semlitsch, 1987b; Semlitsch & Wilbur, 1988). Potentially more stressful conditions from the start of our experiment could have led to higher metamorphosis rates in our “full” (refilled) mesocosms than may have been observed in mesocosms that were full throughout the entire experiment, if we had such a treatment. Regardless, filling mesocosms shifted morphotype expression and enabled both metamorphs and paedomorphs to reach larger masses (Figure 5).

Variation in developmental trajectories is an important adaptation to variable or unpredictable environments, and this plasticity has in part allowed species to colonise diverse habitats with an array of environmental conditions (Bradshaw, 1965; Wilbur, 1980). Because of the critical relationship between individual size and reproductive success, optimising individual phenotype maximises expected fitness (Semlitsch et al., 1988). Plastic responses to environmental variability can enable organisms to adapt to climate change and the increasing prevalence of extreme weather events, as long as such changes do not exceed physiological limits (Hoffmann & Sgrò, 2011). In the variable conditions that characterise temporary ponds, stochastic events such as flooding have the potential to alter not only individual development, but also population growth and community composition by differentially affecting species that occupy distinct niches.

Organisms with highly discrete phenotypes can occupy not only different physical habitats, but also different niches. *Ambystoma talpoideum* illustrates this very well: the three morphotypes have functionally different roles, both ecologically and within the *A. talpoideum* population. Upon emergence, metamorphs move into terrestrial habitats where they feed on terrestrial arthropods, spend much of their time burrowed underground and typically do not mature until their second year (Petranka, 1998). Since both paedomorphs and larvae remain in aquatic habitats, they feed on many of the same taxa (particularly aquatic invertebrates and other larval amphibians), but because paedomorphs are typically larger, they are also able to feed on larger prey. Larvae are unable to breed unless they too become paedomorphic or until after they metamorphose, which could require additional time for maturation in the terrestrial environmental, further delaying breeding. In contrast, paedomorphs are able to breed during their first year, but because of their smaller size, they produce fewer and smaller eggs than mature terrestrial

	Low			Full		
	Metas	Larvae	Paedos	Metas	Larvae	Paedos
Number	↑	○	↓	↓	○	↑
Mass	↓	○	↓	↑	○	↑
Head width	↓	○	○	↑	○	○
SVL	○	○	○	○	○	○
Body condition	○	○	○	○	○	○
Larval period	↓	NA	NA	↑	NA	NA
Growth rate	↑	NA	NA	↓	NA	NA

FIGURE 5 Representation of how filling mesocosms (“full”) affects the development and phenotypic expression relative to “low” mesocosms. Up arrows indicate an increase in that measure, down arrows a decrease. Green indicates the direction of change is beneficial and red indicates detrimental changes. Open blue circles indicate intermediate or neutral effects [Colour figure can be viewed at wileyonlinelibrary.com]

females (Semlitsch, 1985). These differences in maturation timelines mean that each female’s contribution to long-term population growth (over multiple years) can depend in part on the environmental conditions that her offspring experience in their natal habitat and their resulting developmental trajectory.

Abiotic and biotic changes in habitats, such as the filling of ponds and introduction of competitors, can have beneficial, detrimental or potentially interactive effects on resident organisms. The consequences of habitat changes are compounded when considering the plasticity of some organisms, such as *A. talpoideum*, to adjust to these changes. While it is important to understand the causes of phenotypic expression in response to such habitat changes, it is equally important to determine the ecological consequences of changes in phenotypic expression (Miner, Sultan, Morgan, Padilla, & Relyea, 2005). Different phenotypes can occupy unique niches, applying differential predation and competitive pressures on other organisms in the community. While our results show that such abiotic changes can differentially affect plastic organisms, the three morphotypes in the resulting population will each likely have differential effects on their population and community.

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AUTHOR CONTRIBUTION

MRP conceived, designed and conducted the experiment. MRP analysed the data and wrote the manuscript with input from WJR. Both authors gave final approval for publication.

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