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Impacts of hydroperiod on growth and survival of larval amphibians in temporary ponds of Central Pennsylvania, USA

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Abstract The effects of variable hydroperiod (three levels) and initial density of amphibians (two levels) on survival, growth rate, and time to and mass at metamorphosis were studied for wood frogs (*Rana sylvatica*), Jefferson salamanders (*Ambystoma jeffersonianum*), and spotted salamanders (*A. maculatum*). Experiments were carried out in 260-l mesocosms set up outdoors in a forest. These pond simulations were designed to mimic conditions that occur in palustrine temporary wetlands in central Pennsylvania. No animals reached metamorphosis in the short hydroperiod (56 days). However a greater proportion (66%) of tadpoles of *R. sylvatica* survived to the end of the 56-day treatment than the 84- or 158-day treatments (29 and 14%, respectively), from which all survivors metamorphosed. In contrast, neither of the salamanders metamorphosed by 84 days; survival to metamorphosis at 158 days was 15% for *A. jeffersonianum* and 10% for *A. maculatum*. Average instantaneous growth rates for *A. jeffersonianum* decreased with each increase in hydroperiod. Growth of *R. sylvatica* was greater in the 56-day hydroperiod than in hydroperiods of 84 or 158 days. Initial amphibian density had no effect on growth or survival of any species. It appears that salamander larvae were predatory on tadpoles, since survival of *R. sylvatica* was negatively correlated with survival of *A. jeffersonianum* in 84-day treatments and with growth of *A. maculatum* in 158-day treatments.

Key words *Ambystoma* · Mesocosms · Predation · *Rana* · Wetlands

Introduction

Temporary ponds are critical breeding habitats for many amphibians and invertebrates that are adapted to seasonal hydroperiods and the absence of predatory fish (Wiggins et al. 1980). In central Pennsylvania, these wetlands are used exclusively as breeding sites by three species of amphibians, wood frogs (*Rana sylvatica*), Jefferson salamanders (*Ambystoma jeffersonianum*), and spotted salamanders (*A. maculatum*), and as alternate breeding sites by red-spotted newts (*Notophthalmus viridescens*). Hydroperiod, or the duration of standing water, is naturally quite variable temporally and among ponds. For example, in consecutive years we observed complete pond drying as early as the 3rd week of May (3–4 weeks after hatching of *A. maculatum*) and as late as early September (roughly 15 weeks after hatching of *A. maculatum*; Rowe and Dunson 1993). It was unknown what specific impact this variability had on the interactions among larvae or on recruitment of amphibians from this assemblage. It is clear that shortened hydroperiods represent a very harsh environment; we have observed nearly complete reproductive failure in many local ponds due to drought (Rowe and Dunson 1993). Even in years when most ponds retain water into late summer, part of the reproductive output may be lost in those ponds that dry most rapidly.

Previous studies have shown that pond drying may determine such traits as reproductive strategy, growth, recruitment, and timing of and size at metamorphosis of several amphibians (Semlitsch 1985, 1987a; Semlitsch and Gibbons 1985; Semlitsch and Wilbur 1988; Pechmann et al. 1989; Semlitsch and Reyer 1992). In a study using artificial ponds in North Carolina, Wilbur (1987) found that in the absence of competition, *Bufo americanus* tadpoles were able to metamorphose and escape from short hydroperiod (50 days) pools, but not when competition was a factor and food was limiting. Thus it is evident that in some amphibian assemblages hydroperiod is a variable of considerable importance, but there is little information on the impacts of this variable on an

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assemblage of herbivorous and carnivorous species from the north-eastern United States.

In field surveys we have observed large variation in density of egg masses in ponds of the same relative size (Rowe and Dunson 1993). We expected, therefore, that in some situations, food limitation would probably result in competitive interactions among larvae. Competition for resources has been thoroughly investigated for several larval amphibians and amphibian assemblages (Brockleman 1969; Wilbur 1972, 1977, 1982; Wilbur and Collins 1973; Travis 1980; Morin 1981, 1983, 1987; Semlitsch 1987a, b; Morin et al. 1988; Sadinski 1991; Warner et al. 1991, 1993), but empirical tests of the interaction of competition and hydroperiod have less often been undertaken (Semlitsch 1987a, b; Wilbur 1987; Newman 1989; Semlitsch and Reyer 1992). Our assemblage, which consisted both of predatory (*A. jeffersonianum* and *A. maculatum*) and herbivorous (*R. sylvatica*) larvae and predatory adult newts (*N. viridescens*), provided the opportunity to study both competition and predation among amphibians of distinct trophic levels under various combinations of initial density and hydroperiod.

Dunson and Travis (1991) have accused animal ecologists of too often ignoring the potential importance of abiotic variables and interactions with biotic factors that may determine community structure. We designed this study to investigate the importance of an abiotic variable (hydroperiod) and a biotic variable (amphibian density) on survival and growth of amphibians in simulated temporary pond communities.

We advanced the following hypotheses:

1. Competition in high density treatments would result in decreased growth rate, longer larval period, and decreased survival when compared to low density treatments.
2. Survival of amphibians would be increased at longer hydroperiods in proportion to the duration of favorable conditions of water volume.
3. Larval period would be shorter and mass at metamorphosis lower in shorter than in longer hydroperiod treatments, since rapidly degrading conditions in the shortest hydroperiods would favor rapid metamorphosis at a small size (as predicted by Wilbur and Collins 1973).
4. Survival of *R. sylvatica* would be negatively related to growth and survival of predatory *A. jeffersonianum* and *A. maculatum*.
5. Survival of *A. maculatum* would be negatively related to growth and survival of the somewhat larger competitor (and sometimes predator), *A. jeffersonianum*.

Materials and methods

Natural history

The duration and volume of water in temporary ponds are closely linked to climatological conditions. These palustrine wetlands fill in autumn or spring with snowmelt and rainfall and generally dry in mid to late summer, when evapotranspiration increases. The ponds tend to be nutrient poor and often have high Al concentra-

tions. However, the temporary nature of these ponds excludes predatory fish and thus provides a relatively "safe" nursery area for those organisms that are able to take advantage of such sites. The timing of breeding and relatively short duration of aquatic stages of *R. sylvatica*, *A. jeffersonianum*, and *A. maculatum* are adaptations that allow them to exploit temporary habitats. *A. jeffersonianum* typically migrates first to the ponds to breed, followed quickly by *R. sylvatica*, in early spring when the surface ice begins to melt (usually mid to late March). *A. maculatum* follows approximately 2–4 weeks later. Hatching occurs within 3–5 weeks of egg laying, and metamorphosis occurs approximately 6–10 weeks later.

Mesocosm design

We conducted this experiment in 18 plastic wading pools (approximately 1.5 m diameter, 20 cm deep) which we placed in a hardwood forested area near State College, Pa. Since we found no apparent trends in light availability in transects through the area with a hand-held light meter, we haphazardly arranged the pools among trees and randomly assigned them treatments. We filled the pools with approximately 260 l of soft stream water from the headwaters of a nearby mountain stream. We covered them with lids of 2-mm fiberglass window screening to prevent escape or immigration of animals. We constructed traps for metamorphs of 7-l polyethylene containers and window screening and attached them to the pool edges to capture juvenile amphibians and adult newts (Sadinski 1993).

Addition of biotic and abiotic components

In early April, prior to addition of amphibians, we placed 2.2 kg of dry leaves from the surrounding forest floor in all pools to provide substrate and refugia. We identified a subsample of leaves which gave the following proportions: 56% white oak (*Quercus alba*), 22% red oak (*Q. rubra*), 13% bigtooth aspen (*Populus grandidentata*), and 9% red maple (*Acer rubrum*). On the following day, zooplankton, filamentous algae, algae from among the communal egg masses of *R. sylvatica*, and leaves from pond bottoms (with attached periphyton and crustacea) were collected from three temporary ponds. Each component was pooled from the three ponds, mixed thoroughly, and distributed to the pools. To each pool we added 400 ml zooplankton suspension, 40 ml filamentous algae, 30 ml "egg mass" algal suspension, and five pond-bottom leaves. These amounts were chosen based upon prior experiments (Sadinski 1991; Rowe et al. 1992) in which we observed adequate growth and reproduction of these components. While they may not necessarily represent the average relative amounts of these constituents found in natural ponds, the ponds are extremely heterogeneous in their biotic and abiotic characters, and thus the relative amounts we used could certainly be found in some natural situations. We also added 6 g of commercial rabbit food pellets to each pool to provide an additional nutrient base.

Fourteen days prior to addition of amphibians we collected invertebrates from three temporary ponds. We added equal numbers each of fairy shrimp (*Eubranchipus holmani*), mosquito larvae (*Culex* and *Anopheles* spp.), and large copepods (estimated by volume) to each pool. On 28 April (day 1 of the experiment) we collected larvae of *R. sylvatica* (means \pm 1 SE: wet body mass 0.0323 \pm 0.004 g, total length 15.3 \pm 0.6 mm; stage 23–25, Gosner 1960) and *A. jeffersonianum* (wet body mass 0.033 \pm 0.003 g, total length 15.2 \pm 0.4 mm; stage 39–44, Harrison 1969) from three temporary ponds and added them to all pools. Pools assigned to high density treatments received 135 *R. sylvatica* and 24 *A. jeffersonianum* larvae; low density pools received 68 and 12 of each species respectively. Densities were based upon field estimates by Sadinski (1991). On the following day we added adult red spotted newts (*N. viridescens*) collected from four temporary ponds. We placed one male and one female newt in each pool. We removed the newts from all pools between days 83 and 86 following perturba-

tion of metamorph traps by an animal and escape of newts from several pools. This was done to ensure that exposure to this predator was uniform for all treatments.

Because of temporal separation in breeding times, we did not add *A. maculatum* to mesocosms until 19 May (day 21). These animals were hatched in the laboratory from egg masses of the white jelly morph, which is the most common type in our area (see Ruth et al. 1993). We collected egg masses from three temporary ponds and held them in their natal pond water with aeration until hatching and addition to the pools. All larval *A. maculatum* (wet body mass 0.028 ± 0.001 g, total length 16.0 ± 0.2 mm; stage 40–43, Harrison 1969) were pooled, and 60 and 30 individuals were added to each high- and low-density pool respectively.

Adjustment of water volume

For hydroperiod adjustments, we removed water from pools with a bucket and filtered it through 0.5-mm mesh netting to limit removal of organisms. Pools in the 56-day and 84-day treatments were lowered at weekly intervals according to a schedule based on a negative linear regression [change in depth = $-(\text{actual depth}/\text{number of weeks remaining in treatment})$]. Approximately 5 cm (70 l) of water remained at the time of termination of the tests. We did not adjust the volumes of long hydroperiod (158 days) pools until 6 weeks before the end, when a proportional weekly draw-down scheme was initiated so that 5 cm (≈ 70 l) of water would remain at the end of the treatment. We did this to simulate late-season drying of ponds that remained filled throughout the summer. Note that the method of draw-down used here and in most other amphibian studies results in appropriate changes in water level and animal density, but not natural increases in solute concentration such as would accompany evaporation from the ponds (for exceptions see Newman 1989; Tejedo and Reques 1994). However, since water level was lowered weekly and mesocosms were open to evaporation and precipitation, they did experience some effects of these processes.

Sampling for biotic and abiotic components

We collected water samples on days 4, 56, 84, and 158 and analyzed them for pH and specific conductance using laboratory meters, and for [Na], [Ca], [Mg], and [K] on an atomic absorption spectrophotometer following filtration at $0.45 \mu\text{m}$. Samples collected on days 4 and 158 were also analyzed for total Al concentration using the catechol violet method (Dougan and Wilson 1974) following filtration at $0.10 \mu\text{m}$. Those collected on day 158 were additionally analyzed calorimetrically for [NO₃], [PO₄], and [SO₄] using Hach reagents (Hach, Loveland, Colo.).

We checked metamorph traps daily. We returned metamorphs from traps and amphibian larvae that remained at the end of a hydroperiod treatment to the laboratory where we blotted them dry and individually weighed them to the nearest 0.1 mg. We defined metamorphs as having a tail of less than 2 mm (*R. sylvatica*) or as having no remaining gill buds (salamanders). From the measurements of wet mass we calculated the instantaneous relative growth

rate, g , using the equation $g = \ln(\text{final mass}/\text{initial mass})/\text{time}$ (Ricker 1979). Initial mass was the average mass of larvae when introduced to the pools and time was the length of the treatment (for larvae) or length of the larval period (for metamorphs). We made no attempt to subsample animals during the experiment for measurements of size. While such data would provide greater accuracy in determining growth trajectories, such an approach would have been disruptive to the community as a whole and damaging to the amphibians, especially the larval salamanders that rely upon fragile external gills for respiration.

Statistical analyses

We checked data for normality using normal probability plots (Minitab 1989). We examined data for homoscedasticity using Hartley's test for equality of variances (Box 1953; Neter et al. 1990).

We conducted all statistical analyses using Minitab version 7.1 statistical software (Minitab 1989). We determined the individual and interactive effects of initial density and length of hydroperiod on survival, growth rate, and time to and size at metamorphosis (when applicable) for each species using ANOVA. In order to further explore relationships among species, we used the Pearson product moment coefficient (Minitab 1989) to estimate the correlation between growth and survival among species across all treatments and within each hydroperiod treatment, since hydroperiod was found to be the manipulated variable of greatest importance in this study.

We set our experiment-wide type I error rate at $\alpha=0.05$, and adjusted it downward using the sequential Bonferroni adjustment (Rice 1989). Type I error rates were adjusted separately for each ANOVA table. Employing the sequential Bonferroni adjustment we ranked in increasing order the P values obtained from each of the three comparisons per ANOVA table and compared them to critical P values calculated as $0.05/3$, $0.05/2$, $0.05/1$. If the smallest P value from the ANOVA table did not exceed $0.05/3$ it was declared significant and the next larger value was compared to $0.05/2$. We proceeded until a comparison yielded a P value greater than the corresponding critical value, at which point no more results from that table were declared significant. Using this method we also adjusted the critical value for each set of correlation coefficients calculated (15 correlations per "set" calculated within each hydroperiod and over all hydroperiods combined), resulting in adjusted critical P values of $0.05/15$, $0.05/14$, and so on for each set of correlations.

Results

Water chemistry

A summary of water chemistry parameters measured on four sampling dates is given in Table 1. There was some fluctuation in water chemistry throughout the experi-

Table 1 Results of chemical analyses on water samples collected from the mesocosms. All values are presented as means (1 SE). Units of concentration are mg/l unless otherwise noted. Mean pH values were calculated using $[\text{H}^+]$; the SE is expressed in terms of molar H^+ . (– not measured)

Sampling date	pH	Na	K	Mg	Ca	Specific conductance ($\mu\text{S}/\text{cm}$)	A ($\mu\text{g}/\text{l}$)	NO ₃	PO ₄	SO ₄
Day 4	6.68 (6.84×10^{-9})	0.52 (0.01)	4.03 (0.16)	0.49 (0.01)	6.59 (0.26)	47.8 (0.8)	33.5 (1.7)	–	–	–
Day 56	6.68 (3.08×10^{-7})	0.27 (0.02)	6.13 (0.15)	1.87 (0.05)	6.22 (0.13)	69.8 (1.4)	–	–	–	–
Day 84	6.68 (6.84×10^{-7})	0.44 (0.02)	4.63 (0.15)	1.52 (0.04)	4.64 (0.16)	68.5 (1.5)	–	–	–	–
Day 158	6.45 (1.56×10^{-8})	0.38 (0.02)	3.11 (0.12)	0.91 (0.03)	4.06 (0.23)	42.7 (1.2)	29.1 (3.5)	0.15 (0.01)	0.17 (0.01)	0 (0)

Table 2 Results from ANOVA to test for effects of hydroperiod and density on instantaneous growth rate, survival, and time to and mass at metamorphosis of three amphibians. Note that *Ambystoma* metamorphs were only obtained from 158-day hydroperiod treat-

ments, and *Rana sylvatica* metamorphs were obtained only from 84- and 158-day treatments (treatment designations: H hydroperiod, D density). (SS sum of squares for treatment, SSE sum of squares for error, * statistically significant)

Species	Growth	Survival	Time to metamorphosis	Mass at metamorphosis
<i>A. maculatum</i>	H: $F_{2,6}=1.63, P=0.272$ SS=1.569 $\times 10^{-4}$ D: $F_{1,6}=0.31, P=0.598$ SS=2.642 $\times 10^{-5}$ HxD: $F_{2,6}=1.36, P=0.325$ SS=1.309 $\times 10^{-4}$ SSE=2.884 $\times 10^{-4}$	H: $F_{2,12}=4.09, P=0.044$ SS=3.505 D: $F_{1,12}=4.62, P=0.053$ SS=1.982 HxD: $F_{2,12}=0.67, P=0.531$ SS=5.736 $\times 10^{-1}$ SSE=5.147	D: $F_{1,1}=0.33, P=0.667$ SS=10.67 SSE=32.00	D: $F_{1,1}=6.24, P=0.242$ SS=5.358 $\times 10^{-2}$ SSE=8.580 $\times 10^{-3}$
<i>A. jeffersonianum</i>	H: $F_{2,11}=58.52, P<0.001^*$ SS=1.114 $\times 10^{-3}$ D: $F_{1,11}=3.15, P=0.104$ SS=2.998 $\times 10^{-5}$ HxD: $F_{2,11}=2.20, P=0.157$ SS=4.188 $\times 10^{-5}$ SSE=1.047 $\times 10^{-4}$	H: $F_{2,12}=0.84, P=0.454$ SS=2.429 $\times 10^{-1}$ D: $F_{1,12}=5.99, P=0.031$ SS=8.629 $\times 10^{-1}$ HxD: $F_{2,12}=3.45, P=0.065$ SS=9.948 $\times 10^{-1}$ SSE=1.729	D: $F_{1,4}=2.58, P=0.184$ SS=580.20 SSE=900.70	D: $F_{1,4}=2.22, P=0.210$ SS=6.596 $\times 10^{-2}$ SSE=1.186 $\times 10^{-1}$
<i>R. sylvatica</i>	H: $F_{2,12}=25.54, P<0.001^*$ SS=1.777 $\times 10^{-3}$ D: $F_{1,12}=0.17, P=0.687$ SS=5.930 $\times 10^{-6}$ HxD: $F_{2,12}=0.18, P=0.838$ SS=1.246 $\times 10^{-5}$ SSE=4.174 $\times 10^{-4}$	H: $F_{2,12}=20.27, P<0.001^*$ SS=3.683 D: $F_{1,12}=3.33, P=0.093$ SS=3.024 $\times 10^{-1}$ HxD: $F_{2,12}=3.06, P=0.084$ SS=5.563 $\times 10^{-1}$ SSE=1.090	H: $F_{1,8}=0.96, P=0.356$ SS=44.47 D: $F_{1,8}=1.40, P=0.270$ SS=30.40 HxD: $F_{1,8}=0.03, P=0.878$ SS=0.80 SSE=253.65	H: $F_{1,8}=0.01, P=0.998$ SS<1 $\times 10^{-5}$ D: $F_{1,8}=0.60, P=0.460$ SS=1.027 $\times 10^{-2}$ HxD: $F_{1,8}=0.56, P=0.475$ SS=9.580 $\times 10^{-3}$ SSE=1.362 $\times 10^{-1}$

Table 3 Average instantaneous growth rates (day⁻¹), survival (%), time to metamorphosis (days), and wet mass at metamorphosis (g) among hydroperiod treatments for three amphibians. Data were pooled across density treatments. Values are means (1 SE); n=number of tanks from which measurements were made. Different trailing letters within a column indicate those values that differed significantly following multiple comparisons. Proportional values for survival were transformed to arcsines prior to analysis

	A. Growth	<i>A. maculatum</i>	<i>A. jeffersonianum</i>	<i>R. sylvatica</i>
56 days		0.024 (0.003) n=6	0.048 (0.001)a n=6	0.059 (0.001)a n=6
84 days		0.027 (0.003) n=3	0.035 (0.001)b n=5	0.040 (0.002)b n=6
158 days		0.020 (0.002) n=3	0.030 (0.002)c n=6	0.037 (0.003)b n=6
B. Survival				
56 days		40.3 (13.6) n=6	22.2 (6.1) n=6	65.9 (6.4)a n=6
84 days		15.3 (12.4) n=6	31.3 (11.7) n=6	28.5 (8.3)b n=6
158 days		9.5 (6.1) n=6	15.3 (2.8) n=6	13.9 (3.2)b n=6
C. Time to metamorphosis				
84 days		–	–	76 (2) n=6
158 days		143 (3) n=3	111 (7) n=6	72 (2) n=6
D. Mass at metamorphosis				
84 days		–	–	0.585 (0.055) n=6
158 days		0.488 (0.102) n=3	0.854 (0.078) n=6	0.585 (0.047) n=6

ment, but there were no temporal differences in chemical parameters related to any treatment.

Responses to manipulated variables

There were no effects of initial amphibian density on responses of any species. However, hydroperiod significantly affected instantaneous growth rates for both *A. jef-*

fersonianum and *R. sylvatica*, and survival of the latter (Tables 2 and 3). Mass at metamorphosis and time to metamorphosis were independent of manipulated variables for all species (Tables 2 and 3).

Correlative relationships among amphibians

When data for each species were pooled across all treatments, we found that growth rates for *A. jeffersonianum*

were positively correlated with (1) survival of *A. maculatum* ($r=0.646$, $P<0.001$, $n=35$), and (2) growth and survival of *R. sylvatica* ($r=0.814$, $P<0.001$, $n=35$ and $r=0.716$, $P<0.001$, $n=35$ respectively). Growth and survival of *R. sylvatica* were also correlated positively ($r=0.685$, $P<0.001$, $n=36$), and growth of this species was correlated with survival of *A. maculatum* ($r=0.495$, $P=0.003$, $n=36$). We found no significant relationships among species within the short (56 days) hydroperiod treatment, but within the 84-day treatment there was a strong negative relationship between survival of *A. jeffersonianum* and *R. sylvatica* ($r=-0.939$, $P<0.001$, $n=12$). In the long (158 days) hydroperiod, growth of *A. jeffersonianum* was positively correlated with growth and survival of *A. maculatum* ($r=0.925$, $P<0.001$, $n=9$ and $r=0.843$, $P=0.004$, $n=12$ respectively) and survival of *R. sylvatica* and growth of *A. maculatum* were negatively related ($r=-0.955$, $P<0.001$, $n=9$).

Discussion

Interactions among temporary pond organisms and the results of perturbations to a trophic level are dependent upon the abiotic and biotic characteristics of a particular pond. There are a great variety of interactions that must occur among producers, consumers, and predators in a temporary pond. Thus any number of interactions have the potential to be modified by variable pond hydroperiod, and the outcome of these interactions will be determined by the identity of those species that are directly most affected by diminishing water volume. For example, larval caddisflies can be extremely important predators on amphibians, yet they can be temporally quite variable in abundance, possibly as a result of previous pond hydroperiods or other environmental conditions (Rowe et al. 1994).

In most studies using manipulated assemblages of amphibians water chemistry is overlooked as a variable of potential importance, and in many cases these parameters have been unmeasured or unreported (Rowe and Dunson 1994). Thus it is often difficult to discern how well (abiotically) the simulations mimic natural systems and to what degree abiotic parameters may have influenced the results. In this experiment water chemistry presumably had little impact on the results, as the two measured parameters that are known to be toxic to amphibians in some natural situations (low pH and high dissolved aluminum) remained well within tolerable limits (Freda 1986, 1991; Rowe et al. 1992; Sadinski and Dunson 1992; Rowe and Dunson 1993).

Our first hypothesis, that amphibians would be adversely affected by initial density, was not supported by our tests. This indicates that the conditions chosen in this experiment were not extreme enough to result in intra- or interspecific competition among larvae. This result was further supported by the strong positive correlations between growth and survival of wood frogs (intraspecific), and between growth of *A. jeffersonianum* and growth and

survival of *A. maculatum* (interspecific). If intraspecific competition among wood frogs was important in the experiment we would have expected the opposite relationship, low growth rates when survival was high (unless competition was so severe that significant mortality resulted, which is not supported by the results of our density manipulations). Had the salamanders competed interspecifically we would have expected a negative relationship between growth of the two species. While our experimental conditions did not appear to support severe competitive interactions, natural temporary ponds are quite variable in size, hydroperiod, and breeding activity by amphibians (Rowe and Dunson 1993), so it is likely that in some situations both intra- and interspecific competition among these organisms occur.

We hypothesized that increasing hydroperiod would result in increased survival of each species as a result of the duration of high per capita volumes of water in longer duration tanks. However, just the opposite was observed for *R. sylvatica*, and no effect on survival was found for either salamander (Table 3). Of the wood frogs initially introduced 66% survived the short hydroperiod treatment, whereas only 29 and 14% survived the medium and long hydroperiods, respectively (Table 3). All surviving *R. sylvatica* in the short hydroperiod (56 days) treatment were larvae, whereas those from longer duration treatments were metamorphs. Thus the "survivors" from the 56-day treatment would not have been recruited in a natural system, since metamorphosis was not completed by the time of drying. Reduced survival of wood frogs in the longest duration treatments may have been due in part to predation by salamander larvae. In these treatments survival of *R. sylvatica* was negatively correlated with survival of *A. jeffersonianum* (84 days) and growth of *A. maculatum* (158 days), as predicted in hypothesis 4 (Introduction). It appears that, before wood frogs metamorphosed, larval salamanders achieved a size at which they could prey upon tadpoles, thus reducing survival of this species in 84- and 158-day treatments.

Our third hypothesis predicted environmental plasticity favoring truncated larval period and smaller size at metamorphosis in treatments of shorter as compared to longer hydroperiods. Rates of growth for *A. jeffersonianum* and *R. sylvatica* generally decreased with increasing hydroperiod, but this was not the case for *A. maculatum*. Wilbur and Collins (1973) proposed that rapidly degrading conditions, such as are found in drying breeding ponds, should result in a period of decreased growth rate that signals rapid metamorphosis at a smaller size than in ponds that retain water for a longer period. Thus a "trade-off" is expected, in that escape from a deteriorating aquatic environment would result in smaller individuals being recruited to the terrestrial habitat. Such plasticity has been especially well documented for the mole salamander (*Ambystoma talpoideum*) which has been shown to metamorphose from drying ponds while becoming paedomorphic in ponds of constant water volume and presumably less stressful conditions (Semlitsch 1985, 1987a; Semlitsch and Gibbons 1985; Semlitsch

and Wilbur 1988). While we did not obtain salamander metamorphs from 56- or 84-day treatments with which we could compare sizes with those from 158-day treatments, instantaneous growth rates of *A. jeffersonianum* larvae did decrease with each longer hydroperiod.

Growth rates for *R. sylvatica* were also affected by hydroperiod, such that growth was greatest in the 56-day treatment and least in 84- and 158-day treatments (Table 3). No metamorphs were captured from the 56-day treatment to compare with those of longer duration in order that we could test the impact of this difference on size of metamorphs. Since growth data for the short hydroperiod were based upon the size of tadpoles at the end of the treatment, but were based upon sizes of metamorphs for medium and long duration tanks, we view this result with some skepticism. Reductions in mass associated with anuran metamorphosis could have biased this result (see Travis 1980). If a considerable reduction in growth occurred well before metamorphosis (but after the end of the 56-day treatment) we would expect greater growth rates in 56-day tanks than in longer duration tanks in which all survivors transformed. On the other hand an inflection in the growth curve very near the time of metamorphosis should not have influenced the calculated growth rate in the 56-day treatment, since tadpoles removed from this treatment were not yet developmentally near transformation. This difficulty in interpretation does not arise with respect to growth of the salamander (*A. jeffersonianum*) since growth decreased with increasing hydroperiod even in treatments that were truncated long before metamorphosis.

It is evident that pond hydroperiod has an enormous impact on recruitment of amphibians from temporary habitats. Under our experimental conditions, no animals of any species attained metamorphosis within 56 days, and only *R. sylvatica* left the pools within 84 days. We have observed hydroperiods in natural temporary ponds representative of the entire range of hydroperiods tested here. Since hydroperiods often vary among seasons for any particular pond, and among ponds within the same season, periodic natural fluctuations in rainfall and evaporation may severely limit recruitment of amphibians from these wetlands. The community-wide responses of temporary pond organisms to variable hydroperiods remains to be thoroughly studied, and may provide clues as to the indirect ramifications of this variable through the aquatic food web.

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