Pond hydroperiod alters the effect of density-dependent processes on larval anurans

Tracy Noel Rogers and David R. Chalcraft

Abstract: Many studies examine how changes (disturbances) to the abiotic environment alter the intensity of species interactions by directly changing the numbers of individuals involved in the interaction but few studies examine how the abiotic environment affects how strongly individuals interact with each other. We conducted an experiment to evaluate how pond hydroperiod affected the ability of two larval anuran species (*Hyla squirella* and *Bufo terrestris*) to interact with intraspecific and interspecific competitors. Pond hydroperiod altered how an increase in the abundance of intraspecific competitors affected fitness components of *B. terrestris* but not for *H. squirella*. Specifically, an increase in intraspecific abundance caused a reduction in *B. terrestris* survivorship in short hydroperiod ponds but had no effect on fitness components of *B. terrestris* in long hydroperiod ponds. Interspecific competition did not occur between these species in either short or long hydroperiod ponds. Our study highlights the point that the strength of density-dependent processes operating in the aquatic environment can depend on pond hydroperiod. Consequently, the extent to which processes operating in the aquatic environment contribute to the regulation of population and metapopulation size for amphibians will also likely depend on pond hydroperiod.

Résumé : De nombreuses études examinent comment les changements (perturbations) dans l'environnement abiotique modifient l'intensité des interactions entre les espèces en changeant directement le nombre d'individus impliqués dans l'interaction, mais peu de travaux examinent comment l'environnement abiotique affecte la force de l'interaction entre les individus. Nous avons monté une expérience pour évaluer comment l'hydropériode d'un étang affecte la capacité des larves de deux espèces d'anoures (*Hyla squirella* et *Bufo terrestris*) d'interagir avec leurs compétiteurs intraspécifiques et interspécifiques. L'hydropériode de l'étang change la manière par laquelle une augmentation de nombre de compétiteurs intraspécifiques affecte les composantes de la fitness chez *B. terrestris*, mais non chez *H. aquirella*. De façon plus spécifique, une augmentation de l'abondance au sein de l'espèce cause une réduction de la survie de *B. terrestris* dans les étangs à courte hydropériode, mais reste sans effet sur les composantes de la fitness de *B. terrestris* dans les étangs à longue hydropériode. Il ne se produit pas de compétition interspécifique entre ces espèces dans les étangs, que l'hydropériode soit courte ou longue. Notre étude souligne le fait que la force des processus dépendants de la densité en opération dans le milieu aquatique peut dépendre de l'hydropériode de l'étang. En conséquence, l'importance de la contribution des processus en œuvre dans le milieu aquatique à la régulation de la taille de la population et de la métapopulation chez les amphibiens dépendra aussi vraisemblablement de l'hydropériode de l'étang.

[Traduit par la Rédaction]

Introduction

Extensive research demonstrates that both the abiotic environment and biotic interactions have important direct effects on the distribution and abundance of species (for reviews, see Schoener (1983), Sih et al. (1985), and Gurevitch et al. (1992)). Less appreciated, however, are ways that the abiotic environment can alter how biotic interactions affect a species (Dunson and Travis 1991; Chalcraft and Andrews 1999). The abiotic environment can alter biotic interactions in two ways (Wootton 1994; Chalcraft and Andrews 1999). First, the abiotic environment can alter the intensity of either interspecific or intraspecific interactions by changing the abundances of species involved in the interaction. Second, the abiotic environment can change the per capita

effect that either intraspecific or interspecific individuals have on a species (i.e., an environmentally contingent interaction). Although ecologists have devoted much attention to the first mechanism (for reviews on the intermediate disturbance hypothesis, see, e.g., Sousa (1984) and Chesson (2000)), less attention has been directed toward environmentally contingent interactions. Here we examine how an abiotic factor, pond hydroperiod, affects intraspecific and interspecific competitive interactions involving two species of larval anurans.

Hydroperiod and competition have important direct effects on larval anurans. The most obvious effect of hydroperiod is death if larvae do not metamorphose into terrestrial adults before the pond dries. Both hydroperiod and competition also have important effects on growth and

T.N. Rogers and D.R. Chalcraft.[1] Department of Biology, East Carolina University, Greenville, NC 27858, USA.

[1]Corresponding author (e-mail: chalcraftd@ecu.edu).

development of larval anurans. For example, larval anurans tend to metamorphose at smaller sizes in ponds with a shorter hydroperiod (Wilbur 1987; Crump 1989; Laurila and Kujasalo 1999) and in ponds with more competitors (Wilbur 1977, 1982, 1987). Metamorphosing at a smaller mass can decrease adult fitness by lowering survival and fecundity and delaying the onset of sexual maturation (Banks and Beebee 1986; Smith 1987; Berven 1990).

Hydroperiod can also affect the intensity of biotic interactions imposed on larval anurans by altering abundances of predator or competitor species (for review, see Wellborn et al. 1996) or by causing the effects of competitive interactions to be more severe. For example, Wilbur (1987) found that an increase in competitor abundance could slow larval development sufficiently so that no larvae could complete metamorphosis in ponds that dry quickly, while no larvae would die as the result of desiccation in permanent ponds despite reduced developmental rates. Pond drying may intensify competitive interactions by reducing phytoplankton and periphyton abundance (by reducing the volume of water present or the amount of substrate surface area that is underwater), the two major food sources for larval anurans (Alford 1999), while increasing the encounter rate between potential competitors.

Although Wilbur (1987) clearly demonstrated that shortening pond hydroperiod could amplify the intensity of competitive interactions, his study did not separate the effects of interspecific or intraspecific competitors. Tejedo and Reques' (1994) study on the natterjack toad demonstrated that the strength of intraspecific density dependence was stronger in short hydroperiod ponds, but their study only focused on one species and did not examine the influence of hydroperiod on interspecific competition. In our study, we examined how hydroperiod affected the intensity of intraspecific and interspecific interactions involving two species of larval anurans. We hypothesized that pond drying will intensify the effect of intraspecific and interspecific interactions on larval anurans.

Study species

Our study focused on the effects of hydroperiod and intraspecific and interspecific interactions on larvae of *Hyla squirella* (squirrel tree frog) and *Bufo terrestris* (southern toad). Both *H. squirella* and *B. terrestris* are summer breeders that oviposit in ponds with relatively short hydroperiods, but *B. terrestris* will also oviposit in ponds with longer hydroperiods (for review, see Lannoo 2005). Furthermore, both species graze on algae and detritus that are either suspended in the water column or occur on substrates and have comparable larval developmental times (for review, see Lannoo 2005). Given the extensive similarities, it is likely that *H. squirella* and *B. terrestris* are competitors. Although both species are common in the coastal plain of the southeastern USA, little is known regarding how they interact with each other and how these interactions may vary in ponds that differ in hydroperiod.

Materials and methods

Experimental design

We conducted an experiment in 48 artificial ponds (modi-

fied 1100 L Rubbermaid cattle-watering tanks) to evaluate the effect of hydroperiod on the relative strengths of intraspecific and interspecific interactions between *H. squirella* and *B. terrestris*. Control over the experimental conditions in independent and replicate artificial ponds allows investigators to explore complex ecological questions that would otherwise be impractical to study in natural ponds (Chalcraft et al. 2005). Numerous studies suggest that processes identified to be important to the larval ecology of amphibians in artificial ponds similar to ours are also important in natural ponds (Scott 1990; Semlitsch et al. 1996; Resetarits and Fauth 1998).

Our experimental design involved manipulations of the initial abundance of both species in ponds that dried in 50 days (short hydroperiod) and in ponds that did not dry (long hydroperiod). The duration of the short hydroperiod ponds should have allowed most of the tadpoles to metamorphose but under stressful drying conditions, whereas individuals in long hydroperiod ponds did not experience drying conditions. Within each hydroperiod, we established six treatments that differed in the initial abundances of each species: (*i*) no larval anurans of either species, (*ii*) 200 *H. squirella* alone, (*iii*) 400 *H. squirella* alone, (*iv*), 200 *B. terrestris* alone, (*v*) 400 *B. terrestris* alone, and (*vi*) 200 *B. terrestris* and 200 *H. squirella*. This experimental design allowed us to measure (*i*) the effect of intraspecific interactions and (*ii*) the relative effect of intraspecific and interspecific interactions. Treatments without larval anurans allowed us to quantify the availability of algal resources in the absence of grazing larval anurans. The initial densities used in this experiment fell within the range of those observed in natural ponds (Morin 1983; Travis and Trexler 1986; Wilbur 1987). Each of the 12 treatments was replicated four times in a randomized complete block design.

Field techniques

Four groups of 12 closely spaced artificial ponds were placed in an open field at East Carolina University's West Research Campus in Greenville, North Carolina, and each group was identified as a different statistical block. All procedures (e.g., creation, experimental manipulation, and monitoring of ponds) were conducted on a block-by-block basis to minimize within-block variation not attributable to treatment differences. Each artificial pond was equipped with an L-shaped polyvinyl chloride (PVC) standpipe to allow for controlled draining of the pond. The standpipe opening was covered with a screen to prevent unwanted colonization and escape of experimental animals. Ponds were filled with water to a depth of 35 cm on 13–14 May 2006. To add further realism to these artificial ponds, we added 500 g of hardwood leaf litter and an inoculation of algae and zooplankton obtained from a natural pond. Each pond was covered with a tight-fitting fiberglass screen lid to prevent the colonization of unwanted animals and escape of experimental animals.

Larval anurans were obtained from 15 clutches of *H. squirella* and four clutches of *B. terrestris* that were laid 3–6 June 2006. Before the addition of larval anurans to artificial ponds, we randomly assigned a different treatment designation to each artificial pond within each block. Three-day-old larval anurans were randomly assigned to each arti-

ficial pond with the constraint that (*i*) each pond receive a similar proportion of individuals from each clutch to ensure similar levels of genetic diversity within each pond and (*ii*) the number of individuals of each species added to a pond corresponds to the treatment assigned to that pond.

Although all ponds initially had the same depth (35 cm), we simulated drying in short hydroperiod ponds by lowering the L-shaped PVC pipe installed in each pond at predetermined intervals. The rate of drying was based on an equation describing the natural drying curve of ponds located in North Carolina (Wilbur 1987):

$$D_j = 1 - (j/t)^a P$$

where D_j is the desired depth on day j, j is the time in days since the larval anurans were added to ponds, t is the target date in days for the depth to reach zero, P is the depth at the beginning of the experiment, and a is a shape parameter ($a = 2$) for the drying curve.

We quantified algal concentrations present in each pond 40 days after larval anurans were added. A periphyton sample was obtained by scraping algae off a piece of flagging tape tied to a ceramic tile at the bottom of each pond. We recorded the amount of surface area scraped for each sample. A phytoplankton sample was obtained by filtering a known volume of water from each pond. Periphyton and phytoplankton samples were frozen for later chlorophyll extraction using the spectrophotometric methods for chlorophyll *a* described by Clesceri et al. (1998).

Ponds were checked daily, and newly metamorphosed frogs or toads (metamorphs), defined as individuals with at least one forelimb, were removed and returned to the lab. After tail resorption, each metamorph was blotted dry with a damp cloth, measured to the nearest 0.001 g, and then released at the site of egg collection. Larval period of each metamorph was estimated from day of hatching until the date at which it was removed from the pond. Short hydroperiod ponds were terminated on day 50 at a depth of 5 cm as the remaining tadpoles would not likely survive to metamorphose before complete pond drying. Long hydroperiod ponds were terminated on 23 September 2006 (day 104) after all metamorphs emerged. Survivorship for each species was measured as the proportion of individuals added to a pond that successfully metamorphosed. Some larvae survived to the end of the experiment in short hydroperiod ponds but did not complete metamorphosis.

Statistical analyses

Each pond represented an independent experimental unit from which mean larval period, mean mass at metamorphosis, and survivorship to metamorphosis of each species was measured and used for statistical analyses. Survivorship data were log-transformed as this provided a measure of instantaneous per capita mortality rates and homogenized variances. No *B. terrestris* successfully metamorphosed in one replicate of the treatment with a high abundance of *B. terrestris* in a short hydroperiod pond. As a result, we added a nominal value (0.01) to all *B. terrestris* survival data before transfor-

mation so that this observation could be included in the analysis. Excluding this particular treatment from the analysis did not qualitatively change the results. Mass at metamorphosis was log-transformed to meet the assumption of homogeneity of variance. There were no problems with normality of residuals or homogeneity of variances for untransformed values of larval period.

We analyzed our data with analysis of variance (ANOVA) and multivariate analysis of variance (MANOVA). Experimental blocks were treated as random effects in ANOVA and MANOVA models. All other terms in ANOVA and MANOVA models were treated as fixed effects. All analyses were conducted in SYSTAT (version 11.0; Systat Software Inc., Chicago, Illinois). We consider effects to be significant when $p < 0.05$, but we also discuss trends in effects when $p < 0.10$. Summary p values are provided in the manuscript, but the full MANOVA results are available on the Web as supplemental tables.[2]

We tested the hypothesis that hydroperiod alters the effect of increasing intraspecific abundance on a response vector describing larval growth components (larval period and mass at metamorphosis) by conducting a factorial MANOVA for each species with intraspecific abundance (200 vs. 400 larval anurans), hydroperiod (short vs. long), and block specified as the main factors (Smith 1987; Fauth and Resetarits 1991; Chalcraft and Resetarits 2003). These MANOVAs only included data from treatments that did not contain an interspecific competitor, and a significant interaction between intraspecific abundance and hydroperiod supports the hypothesis that hydroperiod alters the effect of increasing intraspecific abundance. Following MANOVA, we used factorial ANOVA, with the same statistical model, to determine if either larval period, mass at metamorphosis, or log survivorship to metamorphosis was affected by these intraspecific treatments.

Similarly, we tested the hypothesis that hydroperiod alters the effects of interspecific interactions on the response vector describing components of larval growth (larval period and mass at metamorphosis) by conducting a factorial MANOVA for each species, with the presence of an interspecific competitor, hydroperiod, and block specified as the main factors. The effect of an interspecific competitor was tested by comparing growth components and survival of a species when it occurred by itself at an initial abundance of 200 individuals versus when that species occurred with a potential interspecific competitor (i.e., treatments with 200 larvae of each species). A significant interaction between the presence of an interspecific competitor and hydroperiod supports the hypothesis that the effect of interspecific interactions changes with hydroperiod. Following MANOVA, we used factorial ANOVA, with the same statistical model, to determine if larval period, mass at metamorphosis, or the log survivorship to metamorphosis was affected by interspecific competitors.

Two additional ANOVAs (one for periphyton and one for phytoplankton) were conducted to evaluate the effects of larval anuran presence, hydroperiod, and their interaction on

the availability of algal resources. The total degrees of freedom for these analyses were reduced because of the loss of three phytoplankton samples and two periphyton samples. When the presence of larval anurans altered algal resources, we performed two additional ANOVAs. One factorial ANOVA evaluated the effects of varying species composition (i.e., *H. squirella* alone vs. *B. terrestris* alone vs. both together) in treatments with 400 larval anurans and the interactive effect between species composition and hydroperiod. The other factorial ANOVA only used data with a single species present and evaluated the effects of species identity (*H. squirella* vs. *B. terrestris*), abundance (200 vs. 400), hydroperiod, and their two-way interactions.

Results

There was a trend for hydroperiod to affect growth components of *B. terrestris* when it occurred by itself, but univariate tests did not detect a significant effect of hydroperiod on either larval period or mass at metamorphosis ($p \geq 0.465$; Supplemental Table S1[2]; Figs. 1a, 1b). Furthermore, growth components of *B. terrestris* were not affected by either intraspecific density or the interaction between intraspecific density and hydroperiod when *B. terrestris* occurred by itself ($p \geq 0.294$; Supplemental Table S1[2]; Figs. 1a, 1b). The influence of intraspecific density on *B. terrestris* survival depended on hydroperiod ($p = 0.009$; Supplemental Table S1[2]; Fig. 1c). Specifically, an increase in *B. terrestris* density reduced survivorship in short hydroperiod ponds ($F_{[1,3]} = 53.356$, $p = 0.005$) but not in long hydroperiod ponds ($F_{[1,3]} = 1.561$, $p = 0.300$). Neither the presence of *H. squirella* nor the interaction between *H. squirella* presence and hydroperiod affected growth components or survival of *B. terrestris* ($p > 0.184$; Supplemental Table S2[2]; Fig. 1).

Although a MANOVA suggested that neither intraspecific density nor hydroperiod nor their interaction affected growth components of *H. squirella* when it occurred by itself, univariate ANOVA indicated that *H. squirella* experienced a decrease in mean mass as conspecific density increased ($p = 0.021$; Supplemental Table S3[2]; Figs. 2a, 2b). Larval period and survival of *H. squirrella* did not differ significantly among treatments that contained only *H. squirrella* ($p \geq 0.152$; Supplemental Table S3[2]; Figs. 2b, 2c). Neither the presence of *B. terrestris* nor the interaction between *B. terrestris* presence and hydroperiod affected growth components or survival of *H. squirella* ($p \geq 0.205$; Supplemental Table S4[2]; Fig. 2).
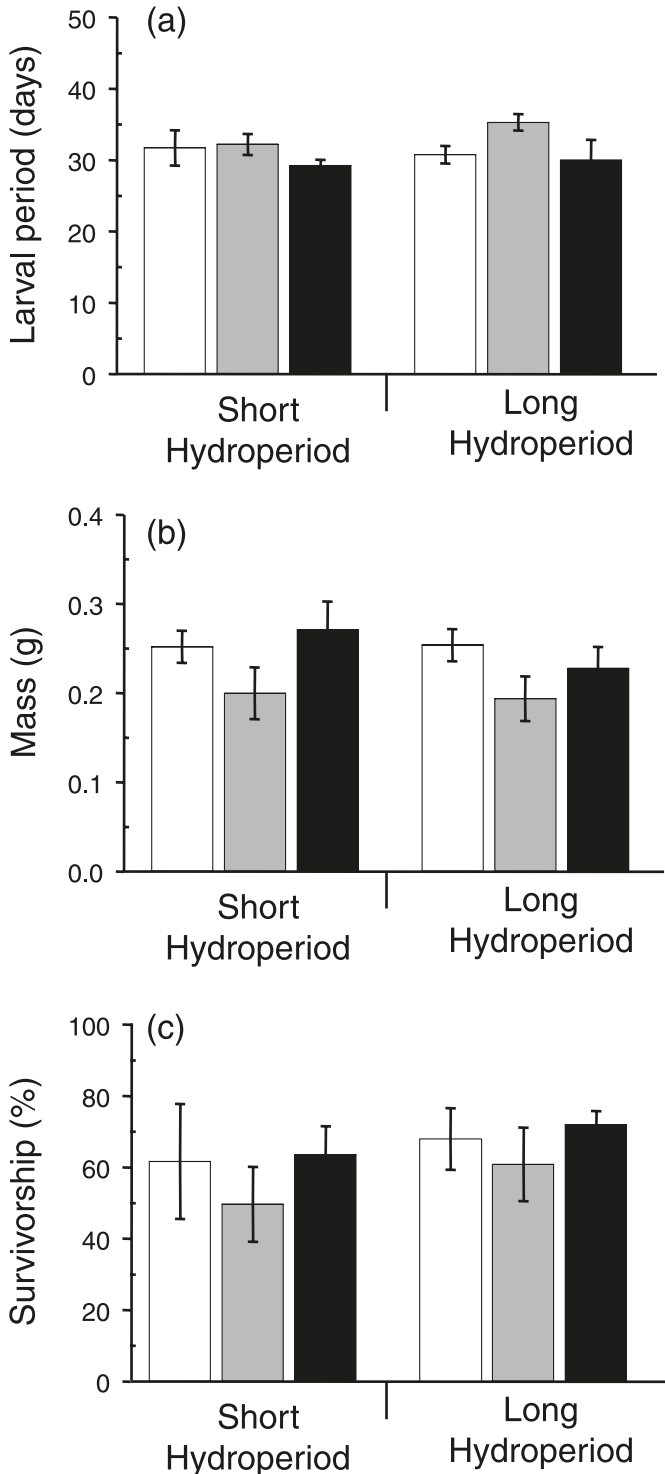
Larval anurans reduced periphyton concentrations ($p = 0.041$; Supplemental Table S5a[2]; Fig. 3a). Although there was a trend for the concentration of periphyton to be greater in long hydroperiod ponds ($p = 0.074$), the interactive effect between larval anuran presence and hydroperiod was not significant ($p > 0.704$; Supplemental Table S5a[2]; Fig. 3a). When 400 larval anurans were present, neither species composition nor hydroperiod nor their interaction affected periphyton concentration ($p \geq 0.168$; Supplemental Table S5b[2]). Neither hydroperiod nor intraspecific density nor species identity nor any of their two-way interactions affected periphyton concentration in treatments that only contained a single larval anuran species ($p \geq 0.187$; Supple-

Fig. 1. (a) Larval period, (b) mass at metamorphosis, and (c) survivorship of *Bufo terrestris* larvae in ponds varying in hydroperiod and the density of potential competitors (open bars, 200 *B. terrestris*; shaded bars, 400 *B. terrestris*; solid bars, 200 *B. terrestris* and 200 *Hyla squirella*). Each bar (±1 standard error) represents the mean of four replicates of a particular treatment.
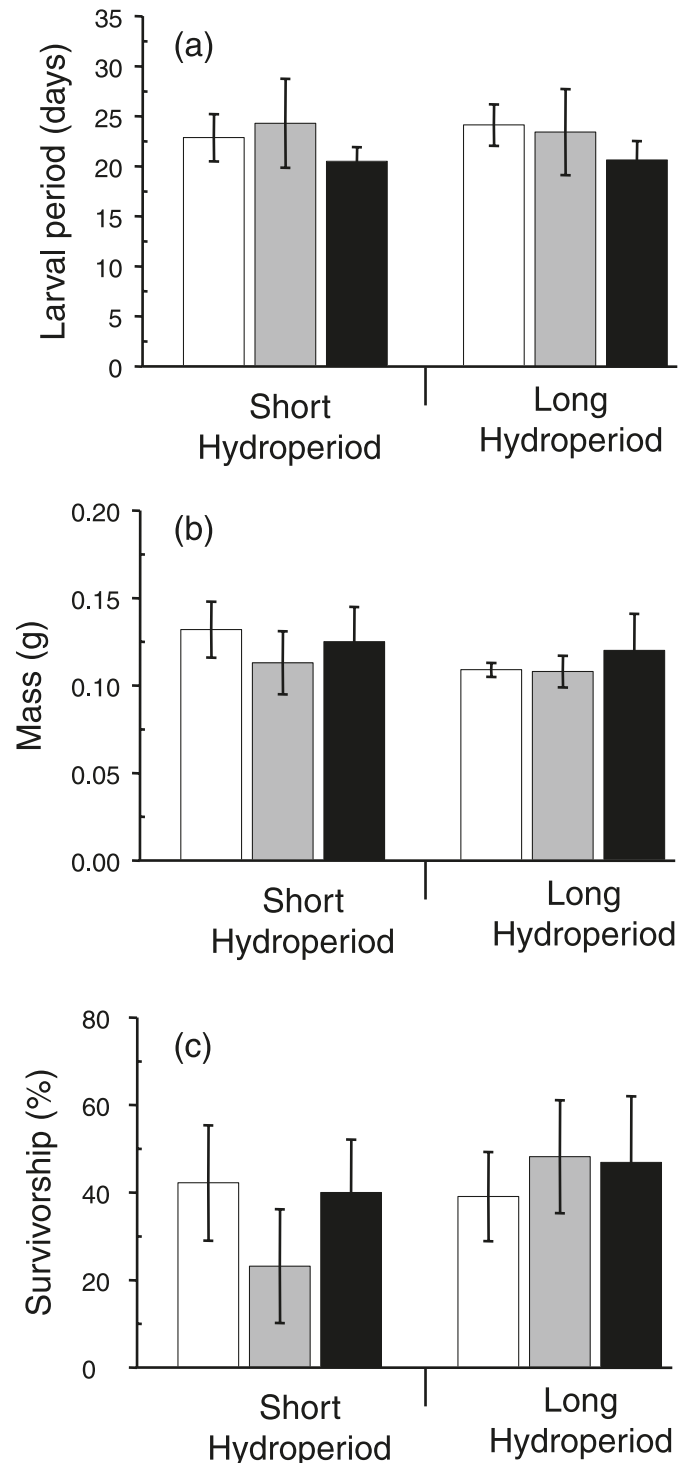
mental Table S5c[2]). Phytoplankton concentration was not altered by the presence of larval anurans, hydroperiod, or their interaction ($p \geq 0.292$; Supplemental Table S5d[2]; Fig. 3b).

Fig. 2. (*a*) Larval period, (*b*) mass at metamorphosis, and (*c*) survivorship of *Hyla squirella* larvae in ponds varying in hydroperiod and the density of potential competitors (open bars, 200 *H. squirella*; shaded bars, 400 *H. squirella*; solid bars, 200 *H. squirella* and 200 *Bufo terrestris*). Each bar (±1 standard error) represents the mean of four replicates of a particular treatment.

Fig. 3. Mean concentration of (*a*) periphyton (±1 standard error) and (*b*) phytoplankton (±1 standard error) collected from short and long hydroperiod ponds that had larval anurans either absent (open bars) or present (shaded bars): $n = 4$ in ponds with no larval anurans; $n = 18$ for periphyton in ponds with larval anurans; $n = 19$ for phytoplankton in long hydroperiod ponds with larval anurans; and $n = 16$ for phytoplankton in short hydroperiod ponds with larval anurans.

Discussion
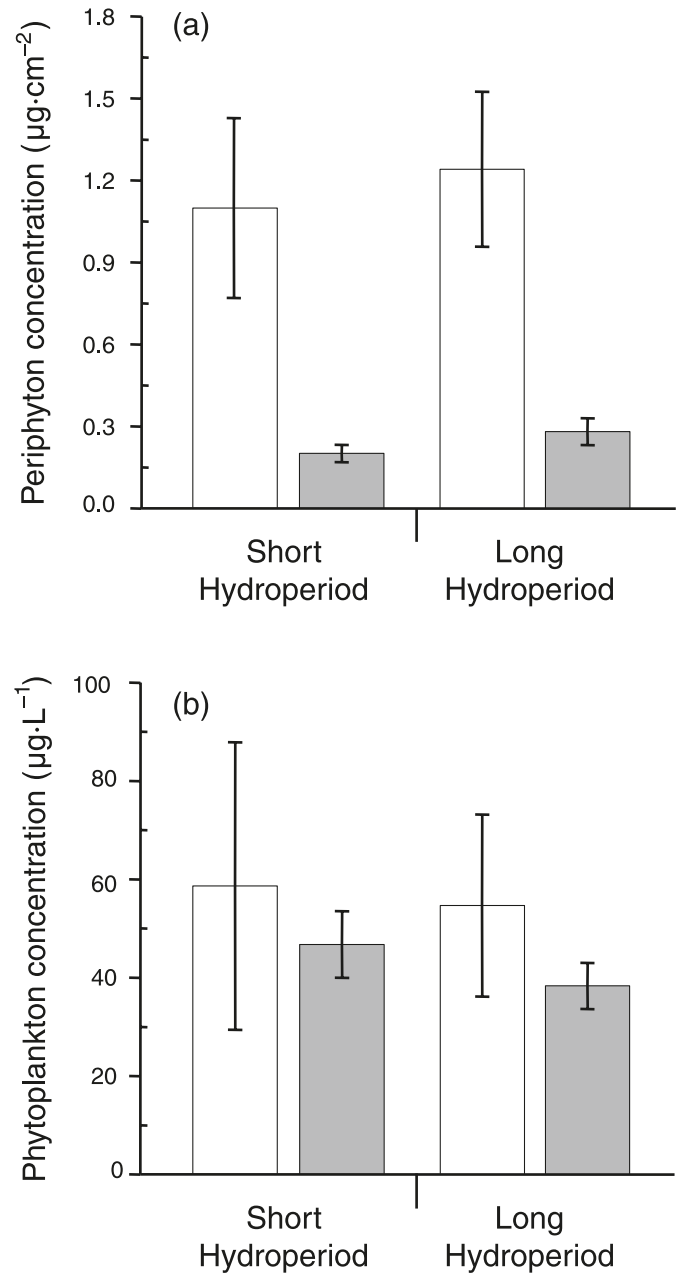
Density-dependent changes in per capita birth, death, or migration rates are essential in maintaining population sizes about some equilibrium value(s). We detected such density-dependent changes during the larval stage of two anuran species. Increasing *H. squirella* abundance reduced *H. squirella* mass at metamorphosis, and prior studies (Banks and Beebee 1986; Smith 1987; Berven 1990) have demonstrated that reduced mass at metamorphosis correlates to reduced fecundity (i.e., per capita birth rates) in many species of larval anurans. Furthermore, increasing the abundance of *B. terrestris* in short hydroperiod ponds resulted in a reduc-

2766

Can. J. Fish. Aquat. Sci. Vol. 65, 2008

tion in the proportion of *B. terrestris* that successfully meta-morphosed from a pond (i.e., per capita death rates). Consequently, variation in the number of larval anurans present alters per capita birth (*H. squirella*) and death rates (*B. terrestris*), which could regulate the population size of these species. Such density dependence during the larval stage has been documented for many anuran species (for reviews, see Alford (1999) and Skelly and Kiesecker (2001)).

Most interestingly, we also found that the strength of intraspecific density dependence depended on the abiotic environment. Specifically, the effect of increasing intraspecific abundance on *B. terrestris* depended on whether intraspecific interactions occurred within a short hydroperiod or a long hydroperiod pond. An increase in the initial abundance of *B. terrestris* caused a decline in their survivorship in short hydroperiod ponds but had no (or very weak) effect on any of their fitness components in long hydroperiod ponds. Although a number of studies are now documenting the extent of spatial and temporal variation in the strength of density-dependent processes (e.g., Bjornstad et al. 1995; Agrawal et al. 2004; Underwood 2007), the source of this variation remains unclear (Agrawal et al. 2004). Our results have identified that a source of variation in the effect of intraspecific density dependence was an abiotic component of the habitat (i.e., hydroperiod).

The effect of the abiotic environment on the strength of intraspecific density dependence is important for at least two reasons. First, it demonstrates that results from studies on biotic processes in one habitat may not necessarily translate to other habitats. During the past 30 years, ecologists have become increasingly aware that the biotic context in which a particular species interaction is measured can actually change the intensity of the species interaction (for reviews, see Wootton (1994) and Werner and Peacor (2003)). Although the dependence of species interactions on the abiotic context was introduced some time ago (Tansley 1917; Park 1954), the importance of such environmentally contingent interactions has not received much consideration. By understanding how the abiotic context affects the intensity of species interactions, spatial and temporal variation in the intensity of biotic interactions become predictable rather than idiosyncratic.

Second, geographic variation in the strength of density-dependent processes that operate during a particular life history stage could change the relative importance of different life history stages to population regulation. The presence of density-dependent interactions among larvae of *B. terrestris* within short but not long hydroperiod ponds suggests that the influence of larval (aquatic) ecology on regulating the size of *B. terrestris* populations will depend on pond hydroperiod. Specifically, larval *B. terrestris* may regulate population size in short hydroperiod ponds, but processes operating on terrestrial phases of *B. terrestris* may be more important in regulating population size at long hydroperiod ponds. Furthermore, the influence of *B. terrestris* larvae on the regulation of metapopulation size may be dependent on the frequency distribution of hydroperiod length among ponds occurring within a metapopulation. If most ponds in a particular metapopulation have a long hydroperiod, the aquatic environment may play only a minor role in regulating the size of the *B. terrestris* metapopulation. Instead, those meta-populations would be influenced more by density dependence occurring during the adult terrestrial stage. Conversely, if most ponds in a particular metapopulation have a short hydroperiod, larval *B. terrestris* may play a much more important role. Alternatively, processes other than intraspecific competition (e.g., predation) may be responsible for regulating larval population sizes of *B. terrestris* in ponds with long hydroperiods.

Why does hydroperiod affect intraspecific interactions among larval *B. terrestris*? We suggest that the increase in the abundance of *B. terrestris* in short hydroperiod ponds causes the total amount of algal food resources available per individual to drop below a threshold value so that proportionately fewer larvae could sustain themselves. This threshold did not appear to be crossed in the long hydroperiod ponds, as survivorship was similar in long hydroperiod ponds that differed in the initial abundance of larval anurans. We have two pieces of evidence for the idea that the total amount of algal food resources available per individual is reduced in short hydroperiod ponds. First, we found that the concentration of periphyton tended to be lower in short hydroperiod ponds. Second, and more importantly, as short hydroperiod ponds dried, there was less submerged surface area available for periphyton growth. Reduced submerged surface area occurred because drying exposed more of the sides of the tanks to the air (5 and 35 cm of a tank side were submerged at the end of the experiment in short and long hydroperiod ponds, respectively). Reductions in submerged surface area also occur as natural ponds dry. Consequently, short hydroperiod ponds had lower total amounts of periphyton present. Thus, an increase in the initial abundance of *B. terrestris* in short hydroperiod ponds means that the amount of food resources per individual is lower in ponds with more larval anurans. An increase in the initial abundance of *B. terrestris* in long hydroperiod ponds does reduce the amount of algal resources per individual, but given the greater abundance of algal resources in long hydroperiod ponds, each individual larva in long hydroperiod ponds would have more food available to it than an individual larva in short hydroperiod ponds. It must be noted, however, that our metric of standing algal biomass may not be an accurate reflection of productivity (i.e., instantaneous rates of biomass production) and other hypotheses could also explain these data.

Hydroperiod altered the effects of intraspecific interactions among *B. terrestris* but not among *H. squirella*. Consequently, hydroperiod does not consistently alter the strength of intraspecific interactions for different anuran species. Our work, in conjunction with the work of Tejedo and Reques (1994), however, suggests that a significant effect of hydroperiod on the strength of intraspecific interactions is not uncommon among anuran species. Further work is necessary to identify properties of species that make their fitness components more susceptible to changes in population abundance in short hydroperiod ponds. One trait that could explain differences in how hydroperiod affects the strength of intraspecific interactions is foraging location. Benthic larval anurans would not really experience a change in the total amount of food resources available in a drying pond because algae that was present higher up in the water column was never really available to them so they are not

losing resources as water volume declines. Microhabitat generalists would experience a decline in resource availability as ponds dry, however, because there is reduced water volume in which algae can grow.

Prior studies of larval anurans in the southeastern US have often documented that interspecific interactions among larval anurans can be relatively intense (for reviews, see Alford (1999) and Skelly and Kiesecker (2001)). The interspecific interactions that we observed between *H. squirella* and *B. terrestris* were weak. Consequently, interspecific interactions during the larval stage likely will not play an important role in determining whether *B. terrestris* and *H. squirella* co-occur. Although other studies suggest that larvae of various *Bufo* species are relatively insensitive to the effects of interspecific interactions (Licht 1967; Wilbur 1977; Richter-Boix et al. 2004), the absence of an interspecific effect of *B. terrestris* on *H. squirella* was surprising; prior studies (e.g., Morin 1983; Wilbur 1987; Fauth and Resetarits 1991) suggest that larval *Bufo* interact strongly with other hylid species. Richardson (2001), however, measured 14 different larval traits in five hylid species from the southeastern US and found that *H. squirella* differed substantially in these traits from the other hylid species that she studied (*H. cinerea*, *H. femoralis*, *H. gratiosa*, and *H. versicolor*). Consequently, these differences in phenotypic traits may explain why *H. squirella* and *B. terrestris* did not interact in similar ways as other hylids do with *B. terrestris*.

Although hydroperiod affected how an increase in intraspecific abundance affected the survival of *B. terrestris*, hydroperiod did not appear to affect the larval growth of either species. This result was rather surprising as both species can often be found in ponds that dry relatively rapidly, and hydroperiod has been found to affect growth in other species that use temporary habitats (e.g., Blaustein et al. 1999). This suggests that these species either lack the ability to detect pond drying or that our "short" hydroperiod length was not sufficiently short to elicit a growth response. Our choice for short hydroperiod duration was based in part, however, on the midpoint of the described larval period for *H. squirella* (for review, see Lannoo 2005) and the fact that this duration was used for other larval anuran studies conducted in the southeastern US (e.g., Wilbur 1987).

In summary, we found that an increase in intraspecific abundance has an important effect on larval performance of two anuran species but that the effect of increasing intraspecific abundance on larval performance can depend on the abiotic environment. The main implications of our study are (*i*) that geographic variation in abiotic conditions can alter the relative importance of particular life history stages to population regulation and (*ii*) that studies of species interactions (e.g., intraspecific competition) conducted under one set of abiotic conditions may not accurately predict the effect of species interactions under a different set of environmental conditions. Our results indicate that a better understanding of how intraspecific and interspecific interactions affect organisms will require more attention to the various mechanisms through which abiotic factors affect ecological communities.

Acknowledgments

References

Agrawal, A.A., Underwood, N., and Stichcombe, J.R. 2004. Intraspecific variation in the strength of density dependence in aphid populations. Ecol. Entomol. **29**: 521–526. doi:10.1111/j.0307-6946.2004.00635.x.

Alford, R.A. 1999. Ecology: resource use, competition, and predation. *In* Tadpoles: the biology of anuran larvae. *Edited by* R.R.W. McDiarmid and R. Altig. University of Chicago Press, Chicago, Illinois. pp. 240–278.

Banks, B., and Beebee, T.J.C. 1986. A comparison of the fecundity of two species of toad (*Bufo bufo* and *Bufo calamita*) from different habitat types in Britain. J. Zool. **208**: 325–338.

Berven, K.A. 1990. Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). Ecology, **71**: 1599–1608. doi:10.2307/1938295.

Bjornstad, O.N., Falck, W., and Stenseth, N.C. 1995. A geographic gradient in small rodent density fluctuations: a statistical modeling approach. Proc. R. Soc. B Biol. Sci. **262**: 127–133. doi:10.1098/rspb.1995.0186.

Blaustein, L., Garb, J.E., Shebitz, D., and Eviatar, N. 1999. Microclimate, developmental plasticity and community structure in artificial temporary ponds. Hydrobiologia, **392**: 187–196. doi:10.1023/A:1003559332439.

Chalcraft, D.R., and Andrews, R.M. 1999. Predation on lizard eggs by ants: species interactions in a variable physical environment. Oecologia (Berl.), **119**: 285–292. doi:10.1007/s004420050788.

Chalcraft, D.R., and Resetarits, W.J., Jr. 2003. Predator identity and ecological impacts: functional redundancy or functional diversity? Ecology, **84**: 2407–2418. doi:10.1890/02-0550.

Chalcraft, D.R., Binckley, C.A., and Resetarits, W.J., Jr. 2005. Experimental venue and estimation of interaction strength: comment. Ecology, **86**: 1061–1067. doi:10.1890/04-0725.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annu. Rev. Ecol. Syst. **31**: 343–366. doi:10.1146/annurev.ecolsys.31.1.343.

Clesceri, L.S., Greenberg, A., and Eaton, A.D. 1998. Section 1020H. Chlorophyll. American Public Health Association, Washington, D.C.

Crump, M.L. 1989. Effect of habitat drying on developmental time and size at metamorphosis in *Hyla pseudopuma*. Copeia, **1989**: 794–797. doi:10.2307/1445521.

Dunson, W.A., and Travis, J. 1991. The role of abiotic factors in community organization. Am. Nat. **138**: 1067–1091. doi:10.1086/285270.

Fauth, J.E., and Resetarits, W.J., Jr. 1991. Interactions between the salamander *Siren intermedia* and the keystone predator *No-*

2768

Can. J. Fish. Aquat. Sci. Vol. 65, 2008

tophthalmus viridescens. Ecology, **72**: 827–838. doi:10.2307/1940585.

Gurevitch, J., Morrow, L.L., Wallace, A., and Walsh, J.S. 1992. A meta-analysis of competition in field experiments. Am. Nat. **140**: 539–572. doi:10.1086/285428.

Lannoo, M. 2005. Amphibian declines: the conservation status of United States species. University of California Press, Berkeley, Calif.

Laurila, A., and Kujasalo, J. 1999. Habitat duration, predation risk and phenotypic plasticity in common frog (*Rana temporaria*) tadpoles. J. Anim. Ecol. **68**: 1123–1132. doi:10.1046/j.1365-2656.1999.00354.x.

Licht, L.E. 1967. Growth inhibition in crowded tadpoles: intraspecific and interspecific effects. Ecology, **48**: 736–745. doi:10.2307/1933731.

Morin, P.J. 1983. Predation, competition, and the composition of larval anuran guilds. Ecol. Monogr. **53**: 119–138. doi:10.2307/1942491.

Park, T. 1954. Experimental studies of interspecies competition. II. Temperature, humidity and competition in two species of *Tribolium*. Physiol. Zool. **27**: 177–238.

Resetarits, W.J., Jr., and Fauth, J.E. 1998. From cattle tanks to Carolina Bays: the utility of model systems for understanding natural communities. *In* Experimental ecology: issues and perspectives. *Edited by* W.J. Resetarits, Jr., and J. Bernardo. Oxford University Press, New York. pp. 133–151.

Richardson, J.M.L. 2001. The relative roles of adaptation and phylogeny in determination of larval traits in diversifying anuran lineages. Am. Nat. **157**: 282–299. doi:10.1086/319196. PMID:18707290.

Richter-Boix, A., Llorente, G.A., and Montori, A. 2004. Responses to competition effects of two anurans according to life-history traits. Oikos, **106**: 39–50. doi:10.1111/j.0030-1299.2004.12743.x.

Schoener, T.W. 1983. Field experiments on interspecific competition. Am. Nat. **122**: 240–285. doi:10.1086/284133.

Scott, D.E. 1990. Effects of larval density in *Ambystoma opacum*: an experiment in large-scale field enclosures. Ecology, **71**: 296–306. doi:10.2307/1940269.

Semlitsch, R.D., Scott, D.E., Pechmann, J.H.K., and Gibbons, J.W. 1996. Structure and dynamics of an amphibian community: evidence from a 16-year study of a natural pond. *In* Long term studies of vertebrate communities. *Edited by* M.L. Cody and J.R. Smallwood. Academic Press, New York. pp. 217–248.

Sih, A., Crowley, P., McPeek, M., Petranka, J.W., and Strohmeier, K. 1985. Predation, competition, and prey communities: a re-

view of field experiments. Annu. Rev. Ecol. Syst. **16**: 269–311. doi:10.1146/annurev.es.16.110185.001413.

Skelly, D.K., and Kiesecker, J.M. 2001. Venue and outcome in ecological experiments: manipulations of larval anurans. Oikos, **94**: 198–208. doi:10.1034/j.1600-0706.2001.t01-1-11105.x.

Smith, D.C. 1987. Adult recruitment in chorus frogs — effects of size and date at metamorphosis. Ecology, **68**: 344–350. doi:10.2307/1939265.

Sousa, W.P. 1984. The role of disturbance in natural communities. Annu. Rev. Ecol. Syst. **15**: 353–391. doi:10.1146/annurev.es.15.110184.002033.

Tansley, A.G. 1917. On competition between *Galium saxatil* L. (G-Hercynium Weig.) and *Galium sylvestre* Poll. (G-asperum Schreb.) on different types of soil. J. Ecol. **5**: 173–179. doi:10.2307/2255655.

Tejedo, M., and Reques, R. 1994. Plasticity in metamorphic traits of natterjack tadpoles: the interactive effects of density and pond duration. Oikos, **71**: 295–304. doi:10.2307/3546278.

Travis, J., and Trexler, J. 1986. Interactions among factors affecting growth, development and survival in experimental populations of *Bufo terrrestris* (Anura: Bufonidae). Oecologia (Berl.), **69**: 110–116. doi:10.1007/BF00399045.

Underwood, N. 2007. Variation in and correlation between intrinsic rate of increase and carrying capacity. Am. Nat. **169**: 136–141. doi:10.1086/509942. PMID:17206592.

Wellborn, G.S., Skelly, D.K., and Werner, E.E. 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annu. Rev. Ecol. Syst. **27**: 337–363. doi:10.1146/annurev.ecolsys.27.1.337.

Werner, E.E., and Peacor, S.D. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology, **84**: 1083–1100. doi:10.1890/0012-9658(2003)084[1083:AROTII]2.0.CO;2.

Wilbur, H. 1977. Density-dependent aspects of growth and metamorphosis in *Bufo americanus*. Ecology, **58**: 196–200. doi:10.2307/1935122.

Wilbur, H.M. 1982. Competition between tadpoles of *Hyla femoralis* and *Hyla gratiosa* in laboratory experiments. Ecology, **63**: 278–282. doi:10.2307/1938942.

Wilbur, H.M. 1987. Regulation of structure in complex systems: experimental temporary pond communities. Ecology, **75**: 151–165. doi:10.2307/2260541.

Wootton, J.T. 1994. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. Ecology, **75**: 151–165. doi:10.2307/1939391.