

Spatial distribution and survival rate of waterfrog tadpoles in relation to biotic and abiotic factors: a field experiment

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Abstract. Predictions about population and community dynamics are usually based on lab experiments. Because the results are difficult to transfer to natural conditions, the major purpose of this study was to test the effects of biotic and abiotic factors on tadpole populations in a natural environment. We stocked six ponds, created the previous year, with known numbers of *Rana esculenta* and *R. lessonae* tadpoles and followed their development over several months. When compared among ponds, tadpole density correlated positively with the nitrate:phosphate ratio. This suggests that water chemistry may have affected survival, either directly or indirectly via productivity. Within ponds, both species showed a clear preference for the shallow zone. This behavior probably reflects a preference for warm water close to the surface, rather than avoidance of predators, because relative densities of odonates also increased from deep to shallow zones. This study is one of few that not only considers the distribution of the anuran tadpoles but the distribution of their predators as well.

Introduction

The factors influencing the structure and dynamics of larval amphibian populations and communities have received a lot of attention. Several studies have shown that growth and survival are density-dependent with competition for food being one of the most important factors (Brockelman, 1969; Wilbur, 1972, 1976). Differential growth rates may not only contribute to unequal competitive abilities but also appear to affect predation risk (Smith-Gill and Gill, 1978; Wilbur, 1980). Most of these studies have been performed in simple laboratory or semi-natural cattle tank environments. Hence, the resulting predictions about population and community dynamics are difficult to transfer to natural conditions. The major purpose of this study was to follow larval development in various fairly natural environments, to quantify potential species-specific differences and to identify their causes by relating growth and survival to differences in biotic and abiotic factors within and among ponds.

The study organisms were waterfrogs of the *Rana esculenta*/*R. lessonae* — complex. They occur in mixed populations with strong dependence of one species on the other. *Rana esculenta* is originally a hybrid between the parental species *R. lessonae* and *R. ridibunda*. In central Europe, however, we find, with some exceptions, only *R. esculenta* and *R. lessonae*. *Rana esculenta* belongs to the rare proportion of vertebrates with clonal or hemiclonal reproduction (Dawley and Bogart, 1989). The hybrid excludes its *lessonae*-genome premeiotically during gametogenesis. The gametes contain only the *ridibunda*-genome which is transmitted clonally (“hybridogenesis”; Schultz, 1969; Tunner, 1973, 1974). Thus, all individuals of one hemiclone share a genetically identical *ridibunda*-genome, and hybrid \times hybrid matings do not lead to viable offspring (Berger, 1971; Binkert, 1981; Semlitsch and Reyer, 1992). Therefore, populations of *R. esculenta* can only persist through sexual parasitism on *R. lessonae*. Depending on locality, the proportion of *R. esculenta* in mixed populations with *R. lessonae* can vary from 7% to 98%, but seems to remain fairly constant through time within ponds (Blankenhorn, 1973, 1977; Berger, 1983, 1990; Hotz and Guex, unpublished data). So far, we do not fully understand which factors determine the relative frequencies of the two taxa and enable their stable coexistence in different ratios (for theoretical explorations see Som et al., 2000; Hellriegel and Reyer, 2000), but predators and environment-specific differences in competitive abilities of larvae are likely candidates. According to cattle tank studies, competition between *R. esculenta* and *R. lessonae* is asymmetric with the outcome depending on the particular ecological conditions. Hybrid tadpoles perform relatively better than tadpoles of the parental species in desiccating ponds, in the absence of predators, at higher densities and/or higher pesticide loads (Semlitsch and Reyer, 1992; Semlitsch, 1993; Horat and Semlitsch, 1994; Fioramonti et al., 1997; Semlitsch et al., 1997), but data on the relative success of the two species under fairly natural conditions are lacking.

For this study, we stocked six ponds, created the previous year, with known numbers of *R. esculenta* and *R. lessonae* tadpoles, followed their development over several months and related it to some features of their biotic and abiotic environment. More specifically we asked: 1) How do physico-chemical factors and predators influence larval development to metamorphosis? 2) Do tadpoles of the two species reduce interspecific competition by distributing themselves over different water depths and, hence, niches? 3) Do the two species differ in larval survival?

Methods

In April and May 1995, we constructed and fenced six ponds, two each in three locations (Ob = Oberrigglatt, Ne = Neftenbach, Ba = Bassersdorf) in the Kanton Zurich (Switzerland). The bottom of each pond was lined with a 2 cm thick mat of argillaceous earth (Bentofix, Geotextil-, Bau- und Umwelt-Technik, St. Gallen, Switzerland) which swells to about 10 cm and becomes impermeable after getting in contact with water. In each location,

R. esculenta in a ratio of 64% to 36% (Negovetic et al., 2000), and all *R. esculenta* belong to the same hemiclone (Hotz, Guex and Semlitsch, unpublished data).

All females ($n = 66$) were injected with fish hormone LHRH (H-7525, Bachem Inc., Bubendorf, Switzerland) to induce synchronous ovulation. On 6 June, right after injection, females — separated by genotype — were brought together with several *R. lessonae* males in tanks (1.04 m \times 1.47 m \times 0.80 m deep) filled with water to a level of 3 cm. After 24 to 48 hours most females had gone through amplexus and released their eggs. The tadpoles hatched 15 June. Five days later, at Gosner stage 25-26 (Gosner, 1960), they were introduced into the six ponds which contained no other anuran species due to the surrounding fences. The *R. esculenta* : *R. lessonae*-ratios among the released tadpoles were 0.71 for all ponds, but absolute numbers of tadpoles (2012-4024) were adjusted to pond water volume in order to achieve similar densities of 340 tadpoles/1000 l. This is well within the range of larval densities reported for many anuran species, including *Rana* (Cecil and Just, 1979; Morin, 1983). Higher densities can be found in shallow water (Petranka, 1989), but are not representative for the pond as a whole. Subsequently, densities of tadpoles and of invertebrate and vertebrate predators were estimated 1, 2, 4, 6, 8 and 10 weeks after releasing the tadpoles. Estimates were achieved by pushing a tube sampler with a base of 1/8 m² down to the bottom of the pond and counting all animals caught in the water column. The tube sampler was handled from a sort of bridge, consisting of flexible shelves, which allowed to sample without walking in the ponds and disturbing the original tadpole distribution. Twenty-one tube samples per pond were taken, seven from each of three depth zones (shallow, intermediate, deep = bottom). Distinguishing between these depth zones allowed to collect data about spatial distribution of the tadpoles within the ponds.

For each sampling week, we estimated the total tadpole number in a pond by multiplying the number of caught tadpoles by a factor which was calculated from the area of that zone covered by water divided by the sampled area (7/8 m²). The sampled area was the area of the tube sampler (1/8 m²) times the number of sampling points (7/depth zone). While the sampled area remained constant throughout the study period, the area of the zone covered by water varied due to the water level and, hence, the pond area changing with rainfall and evaporation. In weeks 8 and 10, when tadpole numbers had already markedly decreased, we sampled additional tadpoles with a dip net to get more tadpoles for a reasonable estimate of the *R. esculenta* : *R. lessonae* (E : L) ratio. The species of each tadpole or metamorphosing froglet was determined by protein electrophoresis (Tunner, 1973). In tadpoles, species identification was based on LDH (lactate dehydrogenase) in tissue, which we obtained by clipping part of the tail fin after anesthetizing the animal with MS222 (Sandoz, Basel, Switzerland). In metamorphs we took lymph from a small incision between two hind toes and analyzed it for albumin. The narcotic caused a mortality rate of less than 1%, tail fin cutting and lymph taking did not cause any mortality in the first 24 hours. Metamorphs trying to leave the fenced pond area were caught in pitfall traps along the fence. They

were measured, weighed and marked with a color injection (Northwest Marine Technology, Washington, USA) into the foot web.

Results

Tadpole development to metamorphosis in relation to abiotic factors and predators

In the first two weeks, the number of tadpoles decreased exponentially to about 1% of those originally released (fig. 2a). Thereafter, the further decrease was fairly low. In week 6, the number of tadpoles must have been underestimated, because it was lower than the number of metamorphosing tadpoles actually counted at the end. The average survivorship of the tadpoles till metamorphosis was only 0.8%.

Of the six ponds originally stocked with tadpoles, five contained survivors in the first two weeks after the release; but their number decreased further. In three out of the six ponds no tadpoles survived at all (fig. 2b) and at the end, only two ponds produced metamorphosing tadpoles. Therefore, we restricted the analysis of biotic and abiotic factors influencing the development to the first two weeks. During these two weeks, the survival rate in the three nutrient poor P-ponds was significantly higher than in the three rich R-ponds ($F_{1,4} = 91.6$, $P < 0.001$, ANOVA).

With respect to biotic factors, survival rate of tadpoles surprisingly seemed to correlate positively with the number of predators (fig. 2b) which consisted mainly of odonates (family Libellulidae), water bugs (family Notonectidae) and newts (family Salamandridae, *Triturus alpestris*) in decreasing order of their frequency. This pattern was similar for the first and for the second week ($r = 0.657$, $n = 6$, $P = 0.133$ and $r = 0.937$, $n = 6$, $P = 0.006$, respectively; Pearson correlation analysis); but both correlations should be viewed with caution since they are mainly due to one pond with extreme predator density.

To test for potential effects of abiotic factors on survival, we first subjected the various measures of water chemistry to a principal component analysis (PCA). It reduced the original 11 variables to 4 factors (table 1). By June, the time when tadpoles grew up, the ponds differed only with respect to the two variables constituting PC3: the three P-ponds with higher tadpole survival had about four times higher $\text{NO}_3:\text{PO}_4$ -ratios than the three R-ponds with lower survival (fig. 2c; $F_{1,4} = 98.762$, $P < 0.001$, ANOVA). This difference was mainly due to significantly higher NO_3 -values in the P- than in the R-ponds ($F_{1,4} = 29.314$, $P = 0.006$), since ponds did not differ in PO_4 -values ($F_{1,4} = 0.542$, $P = 0.502$).

Distribution of the tadpoles with respect to water depth

During the time of our study, all ponds were only one year old and contained very few water plants (*Polygonum amphibium*, *Chara aspera*, *Zannichellia palustris*), with no obvious differences in their amounts between ponds. Hence, there was very little three-dimensional structuring within the water column, and food algae (ca. 80% *Cosmarium*, 20% *Nostoc*)

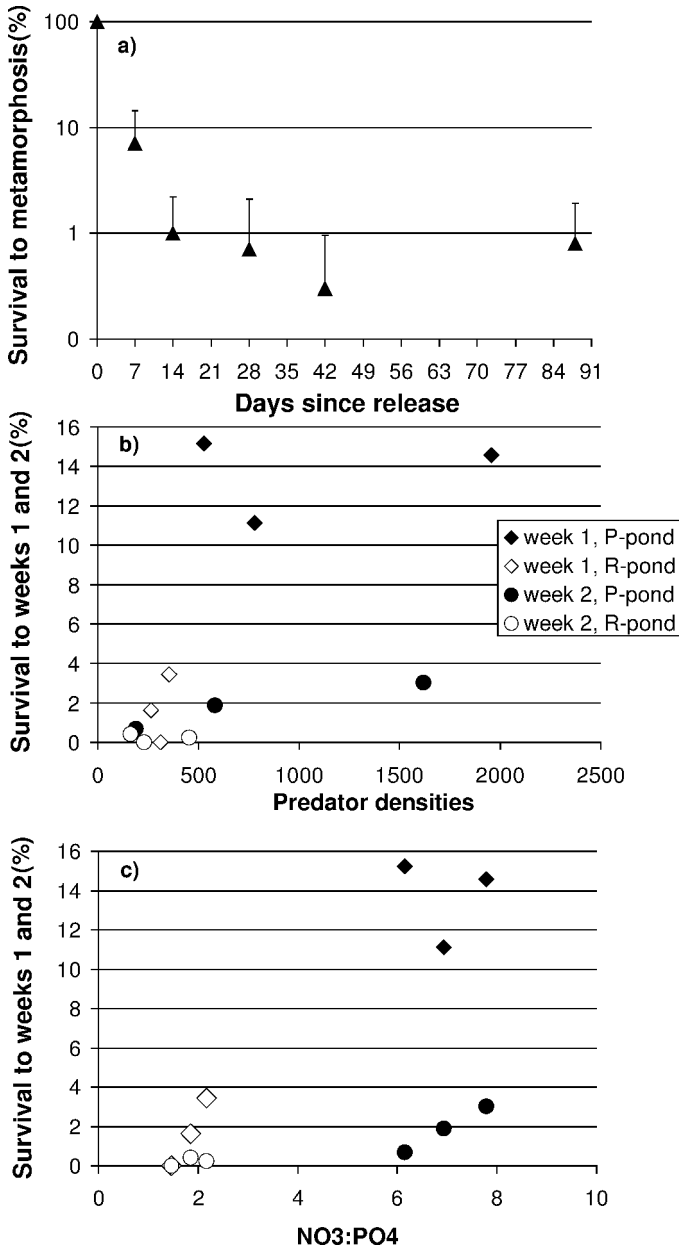


Figure 2. Survival rates of tadpoles in relation to a) time since release into the pond, b) predator density and c) NO₃ : PO₄-ratio. In a) survival to metamorphosis is averaged over all six ponds (mean ± 1 s_{x̄}) and plotted on a log scale. In b) and c) initial survival is plotted separately for week 1 (diamonds) and week 2 (circles) and for ponds which are poor (P-ponds, black symbols) and rich (R-ponds, open symbols) in nutrients, respectively.

were almost exclusively distributed over the pond bottom. Under these conditions, the vast majority of grazing tadpoles are found on the ground (own observations and R. Alford, personal communication). As a result, tube samples from shallow, intermediate and deep areas really reflect densities in the different depth zones, rather than in the water column above them.

In two of the six ponds, we caught too few tadpoles during the first two weeks for analyzing their spatial distribution. In the other four ponds, the number of tadpoles caught decreased from the shallow through the intermediate to the deep zone (fig. 3). Both species showed a clear preference for the shallow zone, no matter whether expectation is calculated from an equal distribution according to the volume ratios 1:3:4 (*R. lessonae*: $\chi^2_2 = 233.9$, $P < 0.001$, *R. esculenta*: $\chi^2_2 = 89.4$, $P < 0.001$) or to the bottom area ratios 1:1:1 (*R. lessonae*: $\chi^2_2 = 43.3$, $P < 0.001$, *R. esculenta*: $\chi^2_2 = 8.1$, $P = 0.02$). There was no difference between the relative numbers of *R. lessonae* and *R. esculenta* recorded in the different water depths ($\chi^2_2 = 5.0$, $P = 0.14$).

This spatial distribution of tadpoles cannot be explained through predator avoidance. When relative larval densities in each of the three depth zones were related to water depth and the proportions of the two major predators in the corresponding zones, depth itself ($F_{2,7} = 4.88$, $P = 0.047$) and relative numbers of odonates ($F_{1,7} = 9.29$, $P = 0.018$) showed a significant effect, whereas *Notonecta* proportions did not ($F_{1,7} = 0.33$, $P = 0.585$; ANCOVA). The relationship with odonates, however, was a positive one: their proportions paralleled those of the tadpoles, with densities decreasing from shallow to

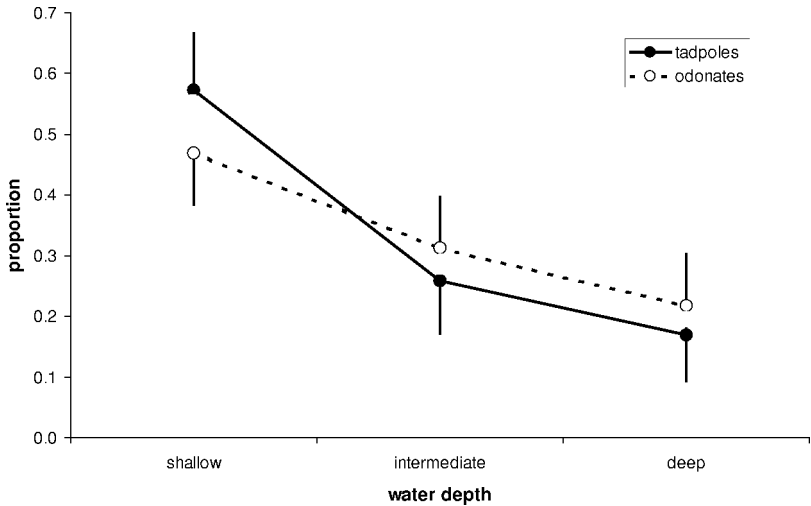


Figure 3. Proportions of tadpoles (dots) and odonates (circles) in relation to the three depth zones: shallow, intermediate and deep water. Shown are means (+ or – one $1 s_{\bar{x}}$) from four ponds, each sampled once during weeks 1 and 2 after releasing the tadpoles. Each sampling consisted of 21 individual tube samplings per pond, 7 from each of the three depth zones.

deep water (fig. 3). Preference for higher temperatures offers a better explanation for this gradient. During daytime, when tadpole distribution was sampled, the upper 10 cm were on average $0.1 \pm 0.06^\circ\text{C}$ (mean ± 1 s) warmer than the deepest regions. This difference is small but significant ($P = 0.025$, $n = 6$; Wilcoxon test).

Tadpoles survival in relation to species

In three out of the six ponds no tadpoles survived at all (fig. 2b). In the other three ponds the *R. esculenta* : *R. lessonae*-ratio remained almost constant from release (0.71 ± 0 ; mean ± 1 s) through later tadpole stages (0.75 ± 0.25) to metamorphosis (0.72 ± 0.09). For none of these three ponds did the ratio change between any two sampling periods (all $\chi_1^2 \geq 0.209$, all $P \geq 0.648$). For one of them the number of metamorphs was too small for a meaningful comparison ($n = 9$); at each of the other two more than 50 tadpoles and metamorphs, respectively, were sampled. In the two ponds, the time to metamorphosis was longer in Neftenbach than in Oberglatt for both species (88 versus 63 days; $F_{1,113} = 251.6$, $P < 0.001$, ANOVA), probably due to the significantly lower water temperature in this pond compared to all the others ($U_{2.5\%[6,9]} = 24.1$, $P < 0.001$, Friedman-Test).

The weight of the metamorphosing tadpoles in these two localities varied with both, pond and genotype (pond \times genotype, $F_{1,113} = 5.0$, $P = 0.037$, ANOVA). *Rana esculenta* had similar weights in Neftenbach and Oberglatt (0.890 g versus 0.706 g), but *R. lessonae* was larger in Neftenbach (0.768 g versus 0.549 g).

Discussion

With 0.8%, the survival rate of the tadpoles till metamorphosis was very low. Multiplied by an annual survival of 10-25% in the first year (R. Altwegg, unpubl. data) and of 53-84% in subsequent years (Holenweg, 1999), this yields a survival rate of about 0.1% from the egg stage to first reproduction. Although 10-20 times lower than the 1-2% reported by Sjögren (1991) for *R. lessonae*, it could still maintain a stable population, if each female laid on average 2000 eggs over her lifetime, which is not an unrealistic assumption (Berger and Uzzell, 1980; Rastogi, 1983; Reyer et al., 1999).

Tadpole survival differed, however, among ponds and was significantly higher in the three P-ponds than in the R-ponds. Since P-ponds also contained more predators than R-ponds, predation cannot be made responsible for pond-to-pond differences in tadpole survival. It is more likely that both predator and prey density correlated with other factors in a similar fashion. Water chemistry and its effect on productivity is a likely candidate (Verma and Prakash, 1991). With no significant differences in PO_4 -values, but higher concentrations of NO_3 , P-ponds with their NO_3 : PO_4 -ratio of about 7:1 came closer to the N:P-ratio of 16:1 that is optimal for primary production (Schwoerbel, 1993) than the R-ponds with a ratio of less than 2:1. Since higher NO_3 -values also increase the proportion of the nutritious green algae (Schwoerbel, 1993), P-ponds may have been more

productive than R-ponds, with the result that both primary consumers like tadpoles and secondary consumers like predators found more food and survived better (cf. Murray, 1990). However, differences in productivity cannot be the only explanation for differences in survival. In one pond, tadpoles had disappeared already one week after releasing them. This cannot be attributed to low productivity and starvation, because at this age tadpoles still have a yolk sac that provides them with enough energy to survive even a further week without feeding (Witschi, 1956).

Thus, not in all ponds may survival have been causally related to water chemistry and productivity. Rather, all these variables may have varied with further unrecorded factors. But whatever the causal factors were, they decreased tadpole survival markedly and, consequently, potentially can impede the establishment of local frog populations in newly created ponds.

The spatial distribution of the *R. esculenta* and *R. lessonae* tadpoles within the ponds was the same; thus, there was no indication of interspecific avoidance or of different ecological niches. Both species preferred the shallow zones in the ponds. This preference cannot be explained through predator avoidance since tadpole proportions were not related to relative numbers of water bugs (*Notonecta*) and even correlated positively with those of dragonfly larvae. Hence, the distribution within ponds supports the above conclusion derived from comparisons between ponds: predators and prey seem to respond to the same factors, probably productivity, which is higher in shallow zones due to more light and warmer water.

Preference for higher temperature has been documented for several anuran species and is usually explained through its benefits in terms of growth rate (Huey and Kingsolver, 1993; Barandun and Reyer, 1997). The temperature response can be confounded, however, by responses to other ecological factors. Alford (1986) found that absolute numbers of two species, *Limnaeodius ocularis* and *Pseudacris ornata*, within a temporary pond in northern Florida were determined by combinations of water temperature, location along the axis of the pond and percent cover by water plants. The latter perhaps indicates predator avoidance as the water plants provide hiding facilities. But even within the temperature niche alone, optimal and preferred temperature may differ between species. In a combined lab and field study, Negovetic et al. (2000) found that *R. esculenta* developed better in colder and *R. lessonae* better in warmer water. This is at odds with the common (but unsupported) belief that the more northern biogeographical distribution of *R. lessonae* is partly due to its higher cold resistance (e.g. Günther, 1990). It is, however, fully consistent with the finding that temperature preference of adult *R. lessonae* lies clearly above that of *R. ridibunda*, the other parental species of *R. esculenta* (Sinsch, 1984), and that among tadpoles the ratio of *R. esculenta* : *R. lessonae* increases with increasing water depth and, hence, decreasing temperature (Negovetic et al., 2000). Our study confirms that water temperature has an impact on the spatial distribution of water frog tadpoles within the pond, but we found no habitat partitioning between the two species on the basis of thermal microhabitat preferences. The most likely explanation is that, with an average difference

of 0.1°C between shallow and deep water, the temperature gradient in the newly created and not very deep ponds were too small to allow segregation.

Although based on a small sample size, our results suggest that in newly created ponds temperature and water chemistry may have a larger impact on distribution and survival than predators. Therefore such ponds, even when they are permanent, seem to differ from older permanent ponds where the — typically numerous — predators are thought to be the most important source of mortality (Skelly, 1996; Wellborn et al., 1996; Williamson and Bull, 1999). Due to the overall low survival rate and the small sample size, no general conclusions can be drawn about differences in development and spatial distribution between the two species. In the only two ponds where sufficient tadpoles were caught, the *R. esculenta* : *R. lessonae* ratio did not change from the egg through the tadpole to the metamorph stage.

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