DENSITY REGULATION IN TADPOLES OF *RANA TEMPORARIA*: A FULL POND FIELD EXPERIMENT

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Abstract. Tadpole density dependence has repeatedly been studied in laboratories and mesocosms, but rarely in natural ponds. The present study manipulated density in three ponds; each pond was divided into one low density section and one high density section. The experiment was run for eight years, switching density treatments within ponds among years. This experimental design cannot definitively separate the experimental density effects from certain lag effects. This problem is discussed. Nonetheless, in all ponds tadpole survival was affected by the density manipulation. The reduced survival of larvae at high density was most pronounced in the pond with the overall highest density. In this pond, the density-dependent mortality almost offset the original, experimental, density difference between sections. Effects on tadpole and metamorph size and development rate were found in those cases in which density-dependent mortality was weak and treatment effects on density persisted to the later stages of tadpole development. However, even if significant, these were generally of small magnitude compared to the variation among ponds and years. I suggest that different modes and degrees of regulation among populations of one species of frog are to be expected, not only due to variation in pond quality but also due to variation in the surrounding terrestrial habitat. This may determine the balance between tadpole and adult population regulation.

Key words: anura; complex life cycle; density regulation; growth rate; intraspecific competition; metamorphosis; population regulation; Rana temporaria; *tadpole.*

INTRODUCTION

The size of animal populations is determined by feedback and nonfeedback mechanisms. Negative feedback mechanisms tend to stabilize a population around some mean number. Identifying these mechanisms helps us understand why population sizes in nature are those that we observe and is thus a key task in animal ecology. However, the task to identify such factors is associated with several complications. I will mention some of those that relate to the study of frogs.

Most frogs have complex life cycles. This means that the tadpole and adult face completely different situations, and the regulating mechanisms, if at all present in both stages, are not likely to be the same (Wilbur 1980). So far, most studies have been concerned with the study of factors that may operate on the tadpole stage (Loman 2001).

Studies of tadpole regulation span a range from simple laboratory setups (Wilbur 1976, Cummins 1989, Loman 1999) to studies in almost natural settings (van Buskirk and Smith 1991, Beebee et al. 1996, Loman 2001). The two approaches complement each other (Scott 1990). The former gives an opportunity to identify the mechanisms that are responsible for density-dependent effects, but there is little guarantee that the effects that are found play an important part in the

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natural regulation of populations (Morin 1998, Polis et al. 1998). Studies manipulating natural ponds are more difficult to interpret, but effects found are more directly related to processes actually influencing natural populations. However, such studies are almost completely lacking (Skelly 2001). Among the few examples are the studies of van Buskirk and Smith (1991), Beebee et al. (1996), and Loman (2001). Other less obvious differences among experimental settings may also lead to conflicting conclusions (Skelly 2002).

Population regulation is ultimately concerned with effects on reproduction and survival. However, this may be difficult to measure and other parameters may well give important information. For example, in frogs, large adults have large clutches (Hönig 1966, Berven 1988, Joly 1991) and large tadpoles have been found to more easily escape from size-limited predators (Richards and Bull 1990, Semlitsch 1990, Tejedo 1993, Lardner and Loman 1995) than small ones. Thus, the study of effects on growth has direct implication for population regulation.

Density regulating factors may well vary geographically, at different scales. The number of predators and density of tadpoles vary by magnitudes among ponds even in restricted areas, creating different scopes for regulating effects (Loman 2002*a*).

With these considerations in mind, the present study occupies the following niche. It addresses the effect of density regulation on the survival, growth, and development of tadpoles. Through carry-over effects on the

adult stage, it also has implications for an understanding of the population dynamics of the species. This approach is not terribly original but is common to most studies of frog population regulation. The study is however unusual because it is completely carried out on free-swimming tadpoles in natural ponds, using the entire ponds and an (almost) natural range of tadpole densities. This means that any effects found can confidently be said to be part of the natural history of real populations of the study species. However, unlike the results of mesocosm experiments, the exact mechanisms cannot be ascertained because of uncontrolled variation among the natural ponds used in the study. Effects on survival, growth, and development are analyzed. The study is carried out in three different ponds, involving three separate populations, and spread out over a period of six to seven years of manipulations. This is too many to expect a consistent result and too few to make any generalizations. The three sites are therefore considered three separate case studies and the evaluation of the results is made accordingly.

The basic approach of the study is to subdivide natural ponds into two sections and redistribute naturally laid spawn so as to create low and high density sections. This is done for a succession of years, switching low and high density sections. Number and size of tadpoles and metamorphs is monitored.

In approach and methods used, this study is similar to a previous study (Loman 2001). There are however three differences. The present study is concerned with the common frog *Rana temporaria*, a close relative to the moor frog *R. arvalis* that was the subject of the previous study. The design of the present study is somewhat simplified in that each pond was divided into two compartments; in the other study there were four. This was motivated by the structure of the ponds involved. Finally, the previous study concerned one moor frog population in one pond while the present involves three different populations and ponds, representing a range of tadpole densities and pond structures. This gives more perspective to the generality of the conclusions. The analysis is somewhat modified and the results more complex, but the results do not contradict those of the previous study.

METHODS

Ponds

Three ponds were used for the study (see Appendix A). They were situated in southwestern (AD17) or central (HP25, HP27) Skåne, the southernmost province of Sweden. Ponds AD17 and HP27 are both situated in open, lightly grazed meadows while HP25 is a forest pond. For this reason HP25 was cooler (Loman 2002*b*) and tadpole development generally slower. The largest pond was HP27 and AD17 had the highest density of eggs and newly hatched tadpoles. All ponds were occasionally affected by drying, usually during the period

of metamorphosis ("truncated metamorphosis," sensu Loman 2002*b*) or in some cases even before the appearance of the first metamorphs. This was especially true for HP25. Although some water always remained in AD17, the water surface was usually substantially reduced in this pond at the time of metamorphosis. *Rana temporaria* was the only anuran present in the study ponds.

In ponds HP25 and HP27, the experiments were conducted from 1991 to 1997 (inclusive). In pond AD17, the experiment was conducted from 1993 to 1998 (inclusive). However, in 1992 and 1993, the two sections of pond HP27 dried at different rates and the affected data were therefore not included. Also, in 1992 (pond HP25), 1993 (ponds AD17 and HP25), and 1995 (pond HP25) one or both sections dried before time for metamorphosis so metamorph data were not analyzed for treatment effects although data available for one section are included in the figures. In 1995, late tadpoles from one of the sections of pond HP25 were badly preserved and could not be satisfactory measured. These are not included in the analysis.

Procedures

The ponds were divided into two sections each by means of a solid tadpole proof fence. Within each pond, the two sections were similar in appearance. In each pond, the fence was erected in the summer of the year before the start of the experiment. Each year, at the time of breeding in spring, all spawn were collected. Within each pond, all spawn were immediately redistributed into two sites, one in each section, in proportions of 1:4. This created in each year one high and one low density section. In consecutive years, high and low density sections were switched. The resulting section densities were within the natural range of densities found in the respective ponds (Appendix B).

Tadpoles were captured at two occasions each year, in the middle of May and at the beginning of June. In each section, period, and year, 3–10 netting samples were taken with a scraper net. The number of samples was dependent on the original size of the ponds and on the actual water surface area present, which differed among years and periods due to drying. Each sample covered 1 m² of pond surface. Body length (snout to vent) and hind leg length of the tadpoles was measured. Hind leg length was divided by body length to give an index of development; a tadpole with long legs relative to body being close to metamorphosis.

At the time of metamorphosis, samples of metamorphs were caught on the shore by hand, measured (body and tail length to 0.1 mm), and released. Metamorphs were used for size measurements as long as traces of the tail were visible. Apart from the size measurement, these captures gave information on time for metamorphosis of each individual. This was considered to have taken place on the day the tail was between 2% and 33% of body length. If the tail was between

33% and 100% of body length, the day after was considered to be the day of metamorphosis. If the tail was longer than the body length, metamorphosis was considered to have taken place two days after. Samples were taken every 3–5 days during the period of metamorphosis. The capture distribution was used to compute median date for metamorphosis for each section and year. Details of the method are described by Loman (2002*b*).

Survival index

The number of eggs laid and the number of tadpoles captured in each netting sample was used to calculate a survival index. Because there were four times as many eggs in the high density sections, the number of tadpoles in a low density sample was first multiplied by four. To compensate for differences in pond area resulting from differences in drying rate among sections, the values were also multiplied by the fraction of the pond area left at the time of sampling. However, if the difference in drying rate between two sections was more than 1:1.5, the data were discarded. This affected the June 1992 and 1993 samples in HP27. In these cases, differences between the sections in the remaining pond habitat could have biased the netting samples. For analysis and graphic representation, $\log_{10}$ values were used. Comparing survival among ponds should be done with caution because differences in bottom structure could affect capture efficiency. However, this problem did not affect comparisons between paired treatments and among years.

Analysis

The study is unbalanced with respect to ponds. The three ponds were not studied in the same years and for various reasons (mainly pond drying) some of the data were also lacking for some ponds in some study years. This meant that several interactions involving ponds could not be analyzed or were difficult to interpret. For this reason, the data were analyzed as three case studies, each based on one of the ponds. Differences between the ponds are suggested, but cannot be tested statistically. Despite being aware of this fact, I will (see *Discussion: Magnitude of density effects and differences in response among ponds*) suggest explanations for these possible among-pond differences.

In all tables, I accounted for the full model, including all possible interactions. If these were not significant, they are printed in italics and the test was rerun without them. If so, the values for the main effects that are printed are those that emerge from the model without interactions.

For two of the ponds it appears that there was a significant effect of the interaction between density treatment and year on survival. This meant that survival in some years was very much lower in the high density section. In turn this resulted in no relation (HP27 in 1991), or even a reversed (AD17 in 1998) relation,

between density intended by design and the actual density in the two sections. Whatever the cause of this variation in survival, this motivated an alternative analysis of tadpole and metamorph performance (growth and development rates). Excluding the extreme years from these two ponds, the interactions between year and density were no longer significant (Appendix D). This alternative analysis answers the following question: Given density differences (that may or may not be part of the actual picture in nature) of advanced tadpoles, is tadpole growth and development affected in ponds that in all other aspects are natural? Note that 1994 was not removed from AD17 despite the fact that it also appeared to be an outlier. However, inclusion of this year did not produce an interaction, so it was deemed compatible with a pattern of consistent density differences between the two section types.

For all response variables, I compute the effect of the treatment separately for each pond. This is based on the ''Estimates of effects'' from the ANOVA; the difference between the estimated values for the variable in high and low density sections, according to the fitted ANOVA model (Wilkinson et al. 1996). The purpose of this is to compare the ponds with respect to effect of the treatment. To also compare the magnitude of the effect of the density treatment with that of pond and year, I computed, with a corresponding method, the estimated means for the two treatments, for three ponds, and for the included years from four main effects ANOVAs (for tadpole length and hind leg length, metamorph length, and date). The outlier years (AD17 in 1998 and HP27 in 1991) were excluded from these computations. For the tadpole data (survival, length, and relative hind leg size), the among-year variation was not considered relevant for the discussion at hand and is therefore not presented. This is because this variation was largely due to differences in the progress of spring temperature, which varies greatly among years.

RESULTS

Effect of density treatment on survival

In all three ponds, the survival was highest in the low density sections (Table 1, Fig. 1). The effect was strongest in pond AD17 and weakest in pond HP25. In pond AD17 the effect of density on survival was, however, not consistent over years and periods. The density treatment effect was more marked in some years (e.g., 1998 and 1995) than in others (e.g., 1997), the treatment effect was more marked in June than in May, and there was a clear difference between May and June in some years (e.g., 1994 and 1995) but not in other years (e.g., 1993 and 1994). Also in pond HP27, the effect of the density treatment on survival differed among years. In pond HP25 no interactions could be detected; however this may be related to the generally lower response altogether. In this pond, survival was highest in the low density section, regardless of year and period

Table 1. Effect of density treatment on tadpole survival in three ponds, and ANOVAs testing effects on tadpole survival.

Parameters	AD17				HP25‡				HP27§			
	Effect†	df	F	P	Effect†	df	F	P	Effect†	df	F	P
Year		5, 119	0.25	0.93		6, 106	6.57	<0.001		4, 132	12.6	<0.001
Period		1, 119	1.33	0.25		1, 106	1.15	0.29		1, 132	3.07	0.082
Treatment	0.72	1, 119	101.2	<0.001	0.19	1, 106	11.1	0.001	0.36	1, 132	54.9	<0.001
Treatment × Year		5, 119	5.20	<0.001		*6, 100*	*0.039*	*0.84*		4, 132	5.88	<0.001
Period × Year		5, 119	3.39	0.007		*6, 94*	*1.10*	*0.37*				
Period × Treatment		1, 119	13.4	<0.001		*1, 93*	*0.20*	*0.65*				

† Effect of density treatment is measured in units of "$\log_{10}$(survival index)." This is the mean difference between survival in low-density and high-density sections.

‡ For HP25, the order of interaction removal is as follows: (1) Period × Treatment, (2) Period × Year, and (3) Treatment × Year. Nonsignificant interactions (in italics) are not included in tests of the main effect.

§ Interactions of Year and Treatment with Period are not tested for pond HP27 because data for June in 1992 and 1993 are missing.

(Table 1, Fig. 1). The estimated survival in high and low density treatments (up to four-fold variation) differed by 0.45 $\log_{10}$ units. This treatment effect was somewhat less than the range of mortality among ponds where populations varied three-fold in density (Appendices A, B, C).

Persistent density effect after manipulation or density compensation

Despite differences in survival, there were more tadpoles captured in the section of pond HP25 that had a high density by design than in that with a low density (Appendix D, Table D1, and Appendix E). In pond HP27, the relative density differed among years; there was a marked numeric effect of the manipulation in all years expect 1991. Disregarding that year, there was no longer an interaction (after Bonferroni correction for three simultaneous tests). Testing the effect without an interaction, there were significantly more tadpoles in the intended high density sections. Also in pond AD17 there was a difference among years in the relative density. In this pond, 1998 was an obvious outlier year. Excluding this year, there was no significant interaction between years and density treatment. Regardless of the inclusion of this year, in this pond the mean differences in density between designed high and low density sections were, however, relatively small and not significant at the time the tadpoles were sampled (Appendix D, Table D1, and Appendix E).

Effects of density treatment on tadpole growth and development

For two of the ponds, AD17 and HP25, the effect of the density treatment on tadpole growth was greater in June than in May (Appendix D, Table D2, and Appendix F, Fig. F1). In the third pond no difference between the periods was evident in this respect. However, to simplify the further analysis I only consider June tadpole body size for all ponds. Only in pond AD17 was there a difference in size between tadpoles from high and low density sections. This was found in addition to a variation among years in this effect. In ponds HP25

and HP27, there was no effect of density on growth rate. These conclusions were true regardless of the inclusion of data from 1998 and 1991.

Because a considerable number of tadpoles had not developed any hind legs at all in May, distorting the distribution, I only analyze June data for this aspect. In AD17, there was a variation among years in the effect of the treatment on development rate, and in addition, there was also a generally faster development in low density sections (Appendix D, Table D3, and Appendix F, Fig. F2). In ponds HP25 and HP27, no significant effects of treatment on development rate were found. However, excluding the outlier year 1991, leg development was slower in high density sections of pond HP27.

The estimated size in high and low density treatments differed by 0.66 mm, which was slightly less than the spread among ponds (Appendix C). This was also true for the difference in relative hind leg length between density treatments (16% vs. 17%).

Effects of density treatment on metamorph size and time for metamorphosis

Metamorphs from low density sections were usually larger than those from high density sections (Appendix D, Table D4, and Appendix F, Fig. F3). However, the effect varied among years, and in pond AD17 it was only significant if the outlier year was excluded.

In two of the ponds (HP25 and HP27), tadpoles from low density sections metamorphosed earlier than those from high density sections (Appendix D, Table D5, and Appendix F, Fig. F4). In the third pond (AD17), there was no effect of density on time for metamorphosis. The conclusions were the same even if the two outlier years were included.

The estimated metamorph size differed by 0.5 mm between high and low density sections. This was less than the spread among ponds and years (Appendix C). This was also true for the difference in time to metamorphosis between density treatments (3.2 d).

Section density

● High
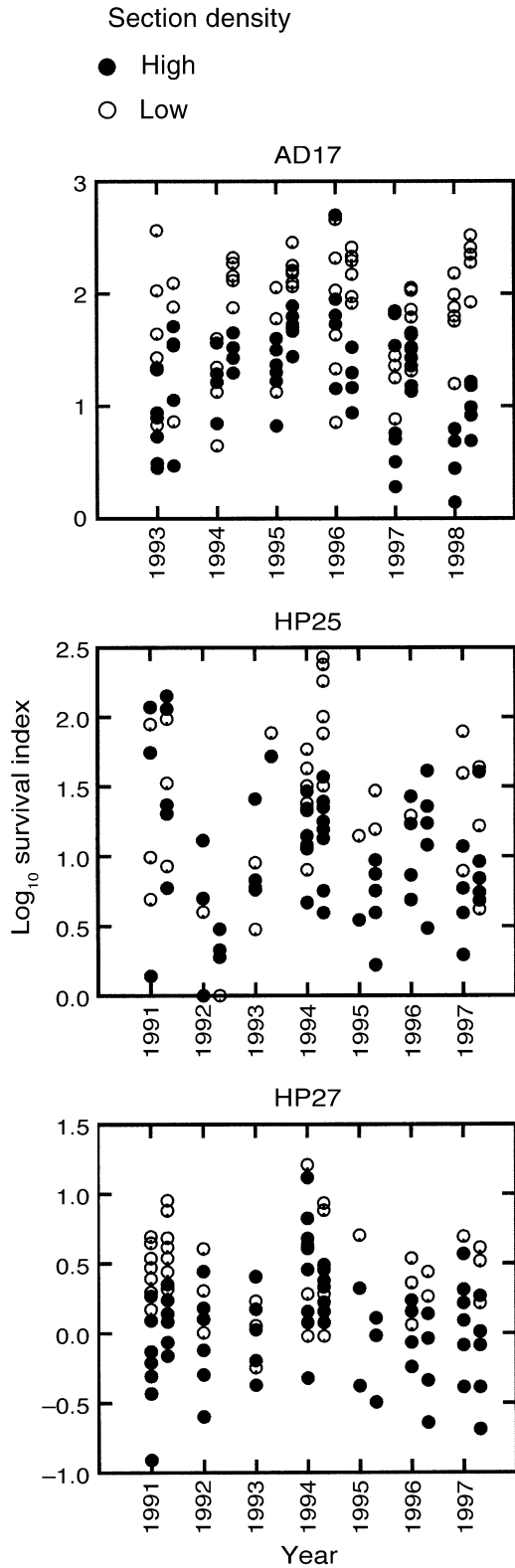○ Low

AD17

HP25

HP27

Year

FIG. 1. Survival from egg to tadpole in high and low density sections is shown. Each data point is based on one netting sample. The number of tadpoles in the sample is used to calculate a survival index (see *Methods: Survival index*).

Autocorrelations

Within each section, autocorrelations of tadpole performance were computed. Out of 22 first order autocorrelations, only one was significant. Out of 18 second order autocorrelations, also one was significant. The frequency of significant autocorrelations (2 for 40 comparisons) is within the realm of chance. However there was a tendency for first order autocorrelation coefficients to be negative (18 out of 22; $\chi^2 = 8.91$, df = 1, $P = 0.003$) as might be expected if the previous year's treatment in a given section had a detrimental effect on the successive year's tadpole performance.

DISCUSSION

Magnitude of density effects and differences in response among ponds

The most striking effect of the density treatment was the effect on survival. This was significant for all three ponds. Survival in the low density section was 5.2 (AD17), 1.5 (HP25), and 2.3 (HP27) times that in high density sections (recomputed from $\log_{10}$ effect values in Table 1). This means that density regulation on the tadpole stage is a reality in the studied populations. Also, some effects of density on tadpole and metamorph growth and development were found. This shows that density regulation may also operate via effects on growth and development rate. These effects were most obvious if years where compensatory mortality had offset the experimental design were excluded. This shows even more clearly that if, for some reason, density differences persist until the late tadpole stage, such effects have the potential to operate at natural densities, in natural ponds. However, the overall magnitude of the effect caused by the density manipulation on tadpole and metamorph performance was not impressive. The magnitudes of the effects were, in general, lower than those resulting from variation among ponds and years in this study. Even larger natural variation in metamorph size and time for metamorphosis was observed in a set of 20 ponds in the same area (Loman 2002*b*). The observations on relative magnitude cannot be statistically tested but put the magnitude of the experimentally induced effects in the context of natural variation. The relatively minor effects on performance are partly an effect of the compensatory mortality taking place at the early part of tadpole growth.

Looking at the three ponds separately, it appears however that tadpoles responded differently to the den-

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Above each year, the left-hand column of data points represents the May samples, and the right-hand column of data points represents the June samples. For pond HP27, data points for June in 1992 and 1993 are not included because high and low density sections dried at different rates, upsetting the intended design.

sity manipulation. In one pond (AD17), there was a strong effect on survival: in fact, by the time tadpoles were sampled there were no significant differences between the high and low density sections. Despite this, there was, at least in some years, also an effect on growth and development rate from the density manipulation. The effect on development rate was limited, as it was only manifest on the tadpole stage, while there was no significant effect on time for metamorphosis. In the other ponds (HP25 and HP27), there were also effects on survival. However these were less drastic than in pond AD17, and in all years the density difference intended by the experimental design persisted at the time of tadpole sampling. Tadpole growth rate and development rate were not affected by the density treatment in these ponds.

In pond AD17, there were no consistent effects of the treatment on the size of metamorphs and also not on the time for their metamorphosis. Possibly, the early differences in density did affect tadpole growth and development but were not strong enough to carry over to the development of metamorphs, because at late tadpole growth differences in survival had leveled out the density differences. In the other two ponds, there were actually effects of the density treatment on both metamorph characters. It seems that the (moderate) density differences that were caused by the experimental treatment finally affected growth and development.

Pond AD17, with a strong effect on survival and some effect, mainly in the short run, on tadpole growth was the pond with the highest initial density of eggs and tadpoles. The densities of eggs and tadpoles were much lower in the other two ponds. This is a possible explanation for the difference in response. Within HP25 and HP27, there was little difference in egg density but because HP25 was shaded, tadpoles grew slower and to a smaller final size. Pond HP27 had the lowest survival rate overall. This may be because this was a pond with a relatively high density of predators (Loman 2002*a*). The overall low survival in this pond may explain the lack of a treatment effect on survival. Thus, different environmental conditions in these two ponds may have caused the same pattern of outcome of the experiment; little effect on tadpole growth and development.

The range of responses on performance found in this study includes those previously found for one population of *Rana arvalis* in the same study area (Loman 2001). In that study, I only found weak effects on tadpole growth and development, but no significant effects on survival.

Alternative interpretations

Could the observed effects on tadpole performance have been caused by, or influenced by, processes other than the experimental density manipulation? It is indeed possible to envisage lag effects (Lande et al. 2002) influencing the performance of the tadpoles. For example, a manipulated high density in a section in year $T - 1$, resulting in high tadpole mortality in this section could here add more nutrients than would be the case in the corresponding low density section with fewer, and possibly better surviving, tadpoles. This condition might in year T support algal growth in the former high (now low) density section, making it more beneficial for tadpole growth than the other section. A second scenario emerges if a high density favors predators in year $T - 1$, increasing their number in year T. This would have the opposite effect, a high density section (in $T - 1$) would in the next year (T, now a low density section) be less favorable for tadpoles. If sufficiently strong, these effects should result in autocorrelations of the performance data. However, no significant autocorrelations were found. However, 18 out of 22 first order autocorrelations were negative. Though this is compatible with the first alternative process suggested above, it is also a pattern inherent in the experimental design, if density dependence is present.

Failure to unequivocally document lag effects does not necessarily mean that they were not present and did not contribute to the effects found, but the design of the study makes it impossible to separate such lag effects from the experimental manipulation. This is because the section trait of "low density in year T" is impossible to separate from the trait of "high density in year $T - 1$." Confounding lag effects would have been avoided if each pond was only used for the experiment in one year. This would have called for more ponds in the study, especially if one wanted to account for year effects (e.g., occasional dry years). Such alternative experimental designs would have been much more demanding logistically than the one chosen. My feeling is that the suggested biases are not important. The first is partly based on the assumption that there is some density effect in the first place, in year $T - 1$. If present, this is merely enhanced by the confounding lag process. The second effect is not likely to be strong because most important predators, newts (*Triturus* sp.) and diving beetle (*Dytiscus*) larvae, have a terrestrial stage between spring seasons and will thus redistribute into the two sections, probably with little regard to tadpole densities.

Other studies

Laboratory studies consistently show density effects on tadpole survival, growth, and development (summarized in Loman 2001). However, the results from field studies are less conclusive. Although Smith (1983), Berven (1990, 1995), and Skelly (1995) have found evidence of density regulation in anuran larvae, other studies (Calef 1973, DeBenedicti 1974, Sredl and Collins 1992) have provided little evidence for such regulation. In full pond experiments at natural densities, Beebee et al. (1996) found little evidence of survival effects on *Bufo calamita* while van Buskirk and Smith (1991) found strong effects on salamander *Ambystoma laterale* survival and growth. In my previous

study on *Rana arvalis* (Loman 2001), density effects on performance were only consistent (but minor) if the (relatively small) effects of compensatory mortality were corrected for. Given the possible range of densities and other factors, it is of course not surprising that no consistent picture emerges. The present study, where the response differed among ponds, within species and geographical region, supports this picture.

Complex life cycles and population regulation

The findings lead to the question of what regulates those populations where no tadpole density effects where found. A likely answer would be adult density effects. However, this subject is much less studied. Apart from Pearson (1955), there appear to be no studies of density effects on adult anurans.

Although I found density-mediated regulation in all study populations, the effects were strongest in pond AD17. Extrapolating, it is expected that density regulation will be absent in low density populations of *Rana temporaria*. Wilbur (1980) emphasizes that variation in the regulating stage can be expected among taxa, and I suggest this should also apply within taxa among populations.

The subject of stage-specific regulation in species with complex life cycles merits a theoretical exploration that so far seems to be lacking. The present study gives a background from real life populations.

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APPENDIX A

A table of pond characteristics is available in ESA's Electronic Data Archive: *Ecological Archives* E085-044-A1.

APPENDIX B

A figure showing natural variation in spawn clumps deposited in the study ponds is available in ESA's Electronic Data Archive: *Ecological Archives* E085-044-A2.

APPENDIX C

A table of tadpole performance by treatment, pond, and year as estimated by main effects ANOVAs is available in ESA's Electronic Data Archive: *Ecological Archives* E085-044-A3.

APPENDIX D

ANOVA tables showing effects of density treatment on tadpole performance (density, tadpole body length, hind leg length, metamorph body length, and time for metamorphosis) in high and low density sections are available in ESA's Electronic Data Archive: *Ecological Archives* E085-044-A4.

APPENDIX E

A figure showing tadpole density in high and low density sections is available in ESA's Electronic Data Archive: *Ecological Archives* E085-044-A5.

APPENDIX F

Figures of tadpole performance (body size, hind leg length, metamorph size, and time for metamorphosis) are available in ESA's Electronic Data Archive: *Ecological Archives* E085-044-A6.