

Rana temporaria metamorph production and population dynamics in the field

Effects of tadpole density, predation and pond drying

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Abstract

This study investigates factors of importance for tadpoles survival and metamorph production in the common frog *Rana temporaria*. It also assesses the importance of this for the population dynamics of the species. Eighteen ponds were studied for up to 8 years. Data collected each year included: number of spawn clumps deposited, tadpole number and metamorph number. The permanency of the ponds was also recorded each year. Measures were taken of predator density. There was no suggestion of density dependence in the survival of tadpoles. In contrast, the number of spawn clumps deposited per pond area was highest for ponds with high survival. Density of predators (sticklebacks, newts and invertebrates) was negatively correlated to tadpole and metamorph survival. This was true both within (among years) and among ponds. Several of the study ponds dried completely before metamorphosis in some years. However, those ponds also were those with the smallest number of predators and in years with successful metamorphosis, these ponds produced more metamorphs than more permanent ponds. An analysis of the year to year dynamics showed that population size (number of deposited spawn clumps) was correlated to that in the previous year, suggesting a fairly high adult survival, but also on the number of metamorphs emerging two or three years before (corresponding to the age of sexual maturity of the species). It is concluded that the aquatic stage is not strongly limiting in these ponds but conservation efforts should be focused on the terrestrial habitat. Also, the study stresses the value of temporary ponds, despite the fact that recruitment often fails totally in these.

Key words: Population regulation, tadpole survival, temporary ponds.

Introduction

Population dynamics is the study of variation in animal numbers. It is concerned with factors that determine population size and its fluctuations over time, including the interrelation of age classes in a population. Factors are of two types. The strength of some factors may be strongly correlated to population size, usually through cause and effect. Sometimes these have been referred to as limiting factors although this can be misleading. These factors are related to what Morris (1959) termed key factors. Examples of such factors are winter temperature that is related to nuthatch breeding population in the following spring (Nilsson 1987) or size of zero age class in some fish (Ricker 1997). Such factors are useful for prediction and their identification also tells us something important about the biology of the species under concern. However

strong the correlation, it is not self evident that these factors are regulating the population. This may or may not be the case. Regulation requires some element of density dependence. Typical examples are litter size in roe deer (Liberg et al. 1991) and fledgling production in great tit (Klomp 1980). The ultimate factor is always some aspect of population density and the proximate factor is some factor of direct consequence for population size; survival or recruitment. The effect may be mediated by other factors like predation, food resources or space, i.e. physical space for barnacles (Connell 1963) or nest sites (Dhondt & Eyckerman 1980).

An old controversy concerns the importance of density dependence for the determination of animal numbers. Presently, most students would agree that some

element of density dependence is present in the regulation of all populations. However, it is still quite possible that some populations usually are below the density limit when this is important and in most years, population densities are determined without the influence of density dependent factors. If present, regulating factors also effect the population, but do not necessarily effect it strongly. It is possible to have density dependent survival of juveniles but in a long lived species, juvenile recruitment may not be very important for the year to year variation in numbers. Note also that the identification of a density dependent factor does not necessarily mean that it is actually regulating the population under study.

Two of the more common candidates as regulating factors are food and predation. The role of food is undisputed although many populations may live at densities where food resources are rarely or never scarce. This is particularly true under constant predation (Connell 1971). The evaluation of predation has changed. The effect on the individual victim is obvious but it is less obvious that regulation is involved. At times predation has been considered a proximate expression of other mechanisms only; the doomed surplus concept (Errington 1946). Also, predation, even if affecting perfectly healthy individuals, may not be density dependent. However, there are numerous examples of predation as a regulating factor, either through switching (Murdoch 1969), where predators turn their attention to the presently most common prey species, or through direct effects on predator numbers (MacLulich 1937).

The identification of effecting and regulating factors has strong implications for the management and conservation of populations. For animals with complex life cycles an extra dimension is added. The different stages are usually dependent on distinct environments. In frogs, e.g. tadpoles are usually aquatic and if important effecting and regulating factors operate on the tadpole stage, the management of aquatic habitats is important for the populations. Alternatively, the important factors may affect the terrestrial juvenile or adult stage.

In frogs, there now exists a substantial amount of long term studies of variation in population numbers (van Gelder & Oomen 1970; Gittins 1983; Loman 1984; van Gelder & Wijnands 1987; Waringer-Löschenkohl 1991; Semb-Johanssen 1992; Sheman & Lorton 1993). These studies have a particular interest as the evidence for a global decline of amphibians is discussed (Blaustein et al. 1994; Alford & Richards 1999; Kiesecker et al. 2001; Pounds 2001). A summary is provided by Houlahan et al. (2000), some support for such a pattern is indeed found. It is also possible to find out, from such data, if the population is actively

regulated, i.e. if the yearly variation in numbers is related to current population size. Such analyses for *Rana temporaria* L. (Meyer et al. 1998) has demonstrated density dependence in numbers. However, such studies do not allow the identification of effecting factors.

Some of the factors that may have an effecting or regulating function in anurans have been studied specifically, without direct reference to changes in population numbers in the field. Numerous laboratory studies have shown density dependence in tadpole survival or growth (Wilbur 1976; Cummins 1989; Loman 1999). There is also evidence from the field of density dependent tadpole survival and performance (Smith 1983; Berven 1990; Loman 2001b). Numerous predators of tadpoles (Semlitsch 1993; Lardner & Loman 1995; Babbitt & Jordan 1996; Zahn 1997) and adult frogs (Licht 1974; Loman 1984; Weber 1989) have been identified. Some studies have also demonstrated that they are quantitatively important in the field (Laurila 1998; Nyström et al. 2001).

The present study asks whether tadpoles survival and metamorphic success in natural ponds are dependent on tadpole competition and/or predation on tadpoles. The importance of variation in metamorph number for the dynamics of the adult population is then assessed. Possible density regulation of the populations as revealed by the year to year variation in adult numbers is not within the scope of this study.

Methods

This study is based on a total of 18 ponds for which data are available on spawn clump numbers, tadpole density and metamorphs production of *R. temporaria*. Data on eggs, tadpoles and metamorphs were collected from 1990 to 1997. However, most ponds were only studied during some of these years. Data on egg numbers were collected until 2000. In addition, data on predator densities were collected at the same time as data on tadpole densities.

Ponds

All ponds are situated in southwestern and central Skåne, the southernmost province of Sweden. They represent a range of pond types. The following types are represented. (1) Old marlpits. These eight are permanent ponds situated in cropped fields. (2) Natural ponds in grazed meadows. These six range in permanency, from temporary (that in dry years dry up completely before time for metamorphosis), to permanent. (3) Natural ponds in forests. These four are all temporary. They also tended to be cooler and metamorphosis

was later in these ponds than in the other types (Loman in press a).

Ponds with fish, except for sticklebacks *Gasterosteus aculeatus*, were excluded from analyses of predator effects. In four of these, juvenile Carussian carps were captured and it was judged that an unknown number of adult fish (with present methods uncapturable), could severely distort the data. In another pond, it was found that it had been stocked with trout.

Size of the pond (m²) was measured each year in spring, at the time of spawning, and again at the times when the tadpole samples were taken. For each pond and year, it was recorded if it had dried before, during, or after the period of metamorphosis (or not at all). These alternatives were given a pond drying index: 0, 1 and 2 respectively. The mean index for a pond was used as a measure of its place on a temporary – permanent scale.

Spawn counts

Each spring, all ponds were searched for frog spawn. This was done several times per season to find all spawn fresh. This made it possible to count the number of clumps and to separate those of *R. temporaria* from those of *Rana arvalis* Nilsson. The number of spawn clumps is considered an index of the breeding frog population associated with the pond. Density of spawn clumps, i.e. clumps per pond area, was used as a measure of competition in the pond. *R. arvalis* was present in 4 ponds. For this measure, the combined density of both *Rana* species was used. The two species have a similar larval ecology and are probably potential competitors as tadpoles (Lardner 1995).

Egg count as a measure of population

The number of eggs found has also been used as an index of the adult population of *R. temporaria* by others (Cooke 1985; Reh 1991; Griffiths & Raper 1994; Kutenkov 1995). It is probably a measure of the number of females breeding in the population because females of this species are considered to produce one clutch (spawn clump) per season (Savage 1961). Using this as an index of the adult population is however more problematic. We can not take for granted that females breed in all years from a certain age and up. However, in a study by Ryser (1989), there was no evidence that adult *R. temporaria* females skip reproduction in some springs. Of course, the problem is partly one of definition but if individual variation in female reproductive pattern is too wide, the use of a definition of adult, based on egg clump production, will be limited for the analysis of population dynamics. However, it was decided that for the purpose of this study, the

available information suggests a good agreement between egg clump variation and number of male and female frogs over a fixed age.

Tadpole densities

Tadpoles were captured twice per year, 12 May to 22 May and 27 May to 8 June, respectively. Within any one year, the total span for sampling all ponds in one period, was always less than seven days. Each capture consisted of, usually, 10 samples with a scraper net. Each sample covered 1 m² pond bottom. More samples were taken in large ponds if tadpole densities were low. Fewer samples were taken in small ponds or in cases where most of the pond was dry at the time of the sampling. The number of tadpoles captured per sample was used as a measure of tadpole density. There was no consistent difference in May and June densities and the average of the two samples was used. However, if the pond had been drying and less than 30% was left in June, only the May value was used. This was done because I considered that effects of drying during the week before the sample could have made it atypical of the pond's condition during the main part of the tadpole period. Tadpole number was estimated as the number of tadpoles per sample (1 m² each) times the present pond area. Tadpoles survival was measured by an index; the number of tadpoles divided by the number of spawn clumps. Some potential problems with this index are mentioned at the end of the last section of the Methods.

Predators

The scraper net samples also yielded potential predators. They were identified into one of 12 groups, that together, covered all animals caught that were considered possible predators (Table 3). Most of these were found to feed on *R. temporaria* tadpoles in a survey by Larder & Loman (1995). The combined number of individuals per scraper net sample was used as an index of predator prevalence in the pond. Each year, the May and June samples were combined, unless less than 30% of pond area remained in June. For these years only, the May sample was used.

The measure of predators is to some extent arbitrary. It is not possible to state, e.g., that one adult *Dytiscus* water beetle is equivalent to one crested newt or one dragon fly larvae. One objective alternative would have been to deduce the best (preserving most information) linear combination predictor by means of a multiple regression or the most robust predictor by means of a stepwise multiple regression. However, a predator index formed in this way can not be used for hypothesis testing in the same study. For this reason,

predator pressure was measured by simply adding all potential predator individuals caught. The fact that this produced significant results supports hypotheses of predator influence on tadpole survival. A similar approach has also been used by others looking for a generalised predator effect (Skelly 1996; Barandun & Reyer 1997).

Metamorph counts

Time for metamorphosis varied among ponds and years (Loman in press a). The earliest recorded metamorph was found on June 6th. In average years and ponds, metamorphosis peaked around June 25th. When metamorphs were expected, each pond was visited once every 2 to 6 days (average inter-search interval 4.1). At each visit, as many metamorphs as possible were captured along the shore of the pond. The searches lasted for 2 to 10 minutes (average search time 6.3 minutes). All metamorphs captured were counted and released at the capture pond. All animals on land were considered to have metamorphosed, regardless of tail length. However, only froglets with a remaining tail over 0.5 mm were considered metamorphs and included in the computation of the metamorph score. To account for the fact that search time and inter-search interval varied, each metamorph captured was weighed by a score, based on two factors. The first was search time for the pond and day. This was total capture time (2 to 10 minutes) minus a handling time of 10 seconds per metamorph captured. If search time was longer, the score for these captures was less. The second was the time elapsed between capture days. If this between-capture interval was longer, up to 6 days, the score for these captures was higher. These scores were adjusted to give a mean weight of 1. Total number of metamorph captures, weighed by the score, was used as an index of metamorph production for the pond and year. Metamorph survival was measured by an index; the metamorph index divided by the number of spawn clumps.

Metamorph index and tadpole number are both indices, not a direct measure of numbers, though tadpole density is more directly linked to actual number. In principle, tadpole density is based on a complete sample of a known area of pond. However, because of differences in pond bottom structure, tussocks, large stones etc, only a fraction of all tadpoles are caught. This fraction is certain to differ among ponds. Among year variation is however likely to be small, only in years when a small portion of the pond was left, because of drying, average bottom structure differed which may have affected the index. Therefore, these years were excluded from the analysis. Dipnet samples

have been used as tadpole density indices by Skelly (1996). Also the metamorph count is an index. As for tadpoles, the proportion of all metamorphs emerging that were actually captured is likely to vary among ponds. This is because the ease with which metamorphs are captured differs among ponds for structural reasons. In addition, no attempt was made to scale the capture effort exactly to shore length of the different ponds. Within ponds though, the search pattern was carried out in a similar way each year. All captures were carried out at day time but variation due to weather were unaccounted for. However, these were

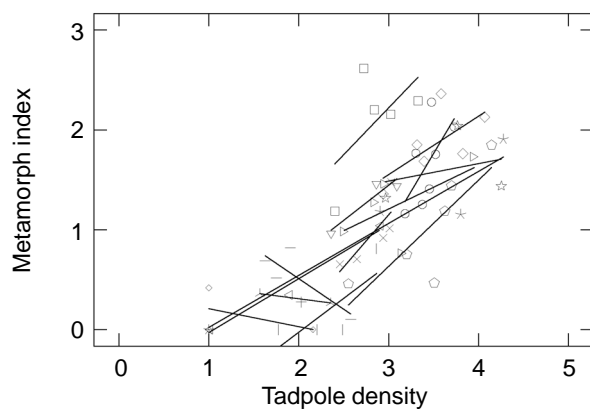


Figure 1. Relationship between metamorphs and tadpole density, accounting for year and pond effects. Values are scaled by a 10 log transformation. Only data from ponds that contained water in June is included. Each point represents data from one pond and one year. Different ponds have different symbols. Within pond linear regressions are shown.

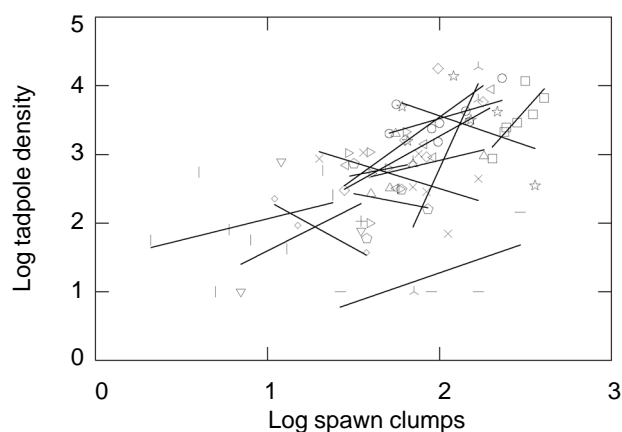


Figure 2. Relationship between tadpole density and number of spawn clumps, accounting for year and pond effects. Values are scaled by a 10 log transformation. Only data from ponds that contained water in June is included. Each point represents data from one pond and one year. Different ponds have different symbols. Within pond linear regressions are shown.

essentially random in relation to pond and year and should to some extent be levelled out because each index was based on several captures on different days. Thus, for the metamorph index, an among pond error was likely, but not an among year error. This is not a problem because for both measures statistical tests including pond as a factor will account for this variation among ponds. A manual count of metamorphs has also been used as an index of production by Licht (1974) and Beebee et al. (1996) while others have used complete samples by means of driftnet and pitfall traps (Berven 1990).

Results

Tadpole and metamorph numbers

The index of metamorph number was strongly correlated to that of tadpole density and also when accounting for effects of pond (Figure 1). This was tested with an ANCOVA, including all years except those where the pond had dried before the time of metamorphosis (tadpole density effect: d.f. = 1:39, $F = 41.2$, $P < 0.001$, pond effect: d.f. = 14:39, $F = 4.72$, $P < 0.001$, year effect: d.f. = 7:39, $F = 1.90$, $P = 0.096$).

Tadpole density was correlated to spawn clump egg number in most ponds (Figure 2). When testing this with an ANCOVA, there was a significant interaction between pond and egg number (d.f. = 13:49, $F = 2.22$,

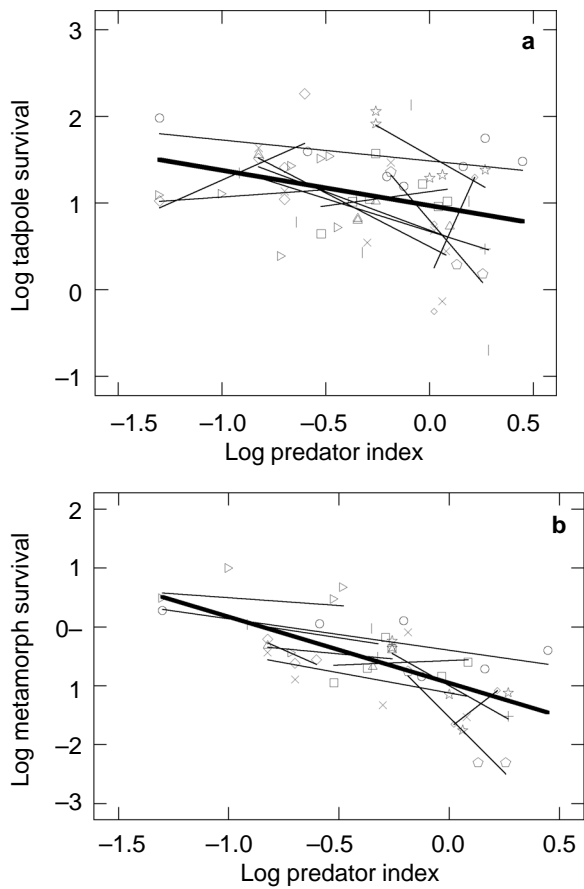


Figure 3. Relationship between predators and tadpole survival (Figure 3a.) and the relationship between predators and metamorph survival (Figure 3b.). Figure 3a.: Tadpole survival is the estimated number of tadpoles in May and June divided by number of eggs laid in the pond. Only data from ponds that contained water in June is included. Figure 3b.: Metamorph survival is the metamorphic index (see methods) divided by the number of eggs laid in the pond. Only data from ponds that had not dried up completely by the time of metamorphosis is included. Predator index is the sum of all predators captured, per netting sample. Values are scaled by a 10 log transformation. Each point represents data from one pond and one year. Different ponds have different symbols. The thick line is a regression of all data points. The thin lines are within pond linear regressions.

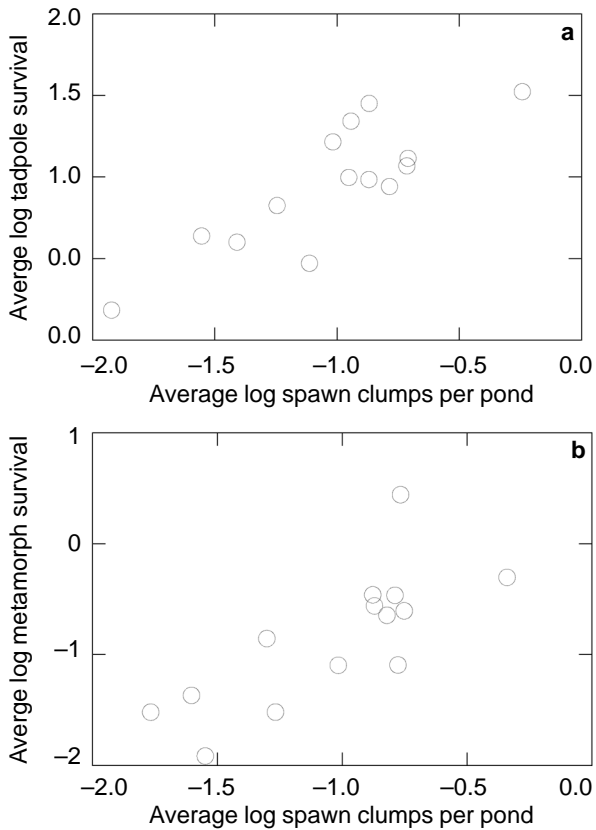


Figure 4. Relationship between density and tadpole survival (Figure 4a.) and the relationship between density and metamorph survival (Figure 4b.). Response variables as explained in Figure 3. Density is measured as number of spawn clumps per pond area. Values are scaled by a 10 log transformation. Each point represents the average value for one pond, over all years of study. This is in contrast to Figure 3. Although the two figures are based on the same type of data, the focus has been changed. For predators, Figure 3., there was a within pond effect that is emphasised by the within pond linear regressions. For density (Figure 4.) there is no such effect. However, in this case there is an among pond effect, emphasised by showing the average pond values.

$P = 0.022$). The four ponds with a negative slope (Figure 2.) tended to have high predator density and low egg density. These effects were however not significant when tested by the Pearson correlation coefficient between slope and predator index ($N = 10, r = -0.53, P = 0.12$) and egg density ($N = 14, r = 0.23, P = 0.42$), respectively. If the interaction is disregarded, there were significant effects of both egg number (d.f. = 1:62, $F = 5.83, P = 0.019$) and pond (d.f. = 14:62, $F = 4.16, P < 0.001$) on tadpole density. There was no corresponding, significant, effect of egg number on the metamorph index (interaction: d.f. = 14:33, $F = 0.92, P = 0.55$, simple egg effect: d.f. = 1:46, $F = 0.15, P = 0.70$, simple pond effect: d.f. = 14:46, $F = 6.41, P < 0.001$).

The pond effects on tadpole and metamorph numbers represented in part methodological effects, as discussed in the methods section, but could also represent variation in traits among the ponds. The effect of variation in two traits, predator index and egg density (com-

petition) was analysed with two way ANOVAs. These factors were both potential causes of the variation in tadpole and metamorph survival because there was a significant variation among ponds (d.f. = 10:41, $F = 3.74, P = 0.0013$) and years (d.f. = 7:41, $F = 5.79, P < 0.001$) in predator index and among ponds (d.f. = 14:125, $F = 11.2, P < 0.001$) but not year (d.f. = 12:125, $F = 0.71, P = 0.83$) in egg density.

Thus, there was an overall correlation between predator index and tadpole (Figure 3a) or metamorph (Figure 3b) survival; lower survival at higher predator densities, (correlation of average pond values: $N = 11, r = -0.63, P = 0.037$ and $N = 11, r = -0.87, P < 0.001$, respectively). These effects were also present within pond, in addition to pond effects (tested with ANCOVA, Table 1 top half). There was also a corresponding overall correlation between egg density and tadpole (Figure 4a) or metamorph survival (Figure 4b); higher survival at higher egg densities (one data point per pond: tadpole survival: $N = 14, r = 0.83, P < 0.001$,

Table 1. Effect of predators and density on tadpole and metamorph survival. Predators and density are each tested with a two-way ANCOVA which, in addition to predators or density, includes pond as a factor.

Effect of:	On:	Category (pond)			Covariate (predation or density)		
		d.f.	F	P	d.f.	F	P
Predation	Tadpole surv.	10:45	2.00	0.055	1:45	5.50	0.024
	Metamorph surv.	10:30	2.92	0.012	1:30	7.51	0.010
Density	Tadpole surv.	14:62	2.73	0.003	1:62	0.39	0.53
	Metamorph surv.	14:46	3.80	< 0.001	1:46	0.73	0.40

Table 2. Outcome of six ANCOVAs (one column each) testing effects of year, pond and past population size on current population size. Current population size is measured as number of egg clumps laid in spring in a pond. Past population size is either adult population 1, 2 or 3 springs before current (lag = T-1, T-2 or T-3) or the number of recruits in the summer 1, 2 or 3 years before. Adult population is estimated by the number of egg clumps laid. Recruits is estimated by the metamorph index.

	Lag	Adult			Recruits		
		T-1	T-2	T-3	T-1	T-2	T-3
Year	d.f.	11:114	10:101	9:87	7:54	7:50	7:46
	F	1.84	1.00	1.52	2.11	3.62	0.95
	P	0.055	0.45	0.15	0.058	0.0031	0.47
Pond	d.f.	15:114	15:101	15:87	15:54	15:50	15:46
	F	3.43	2.82	5.09	18.9	14.7	12.3
	P	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Population (adults or recruits)	d.f.	1:114	1:101	1:87	1:54	1:38	1:46
	F	11.5	7.05	2.52	3.06	4.33	5.91
	P	< 0.001	0.0092	0.11	0.086*	0.043	0.019

* This non significant relation is negative, less egg clumps the more recruits.

metamorph survival: $N = 14$, $r = 0.77$, $P = 0.001$). However, these effects were not present within ponds (tested with ANCOVA, Table 1 bottom half).

Breeding population densities

The egg (spawn clumps) count in one year was correlated to the count in the year before (egg count is used as an index of breeding population density) (Figure 5). This was significant when tested with an ANCOVA that also accounted for pond and year effects (Table 2). There was also a tendency for a year effect. The egg count was also correlated to that two years before but not to that three years before. The egg count was not

correlated to the metamorph index in the year before. There were correlations to the metamorph index two and three years before (Table 2; Figure 6). The year effect was significant in the test of indices lagging two years behind. The pond effect was significant in all six tests.

Predators and pond drying

There were more predators in permanent ponds than in those that frequently dried before tadpole metamorphosis (temporary ponds) (Figure 7, Spearman rank correlation test, $N = 15$, $r_s = 0.92$, $P < 0.01$). Looking at individual predator groups, most showed the same ten-

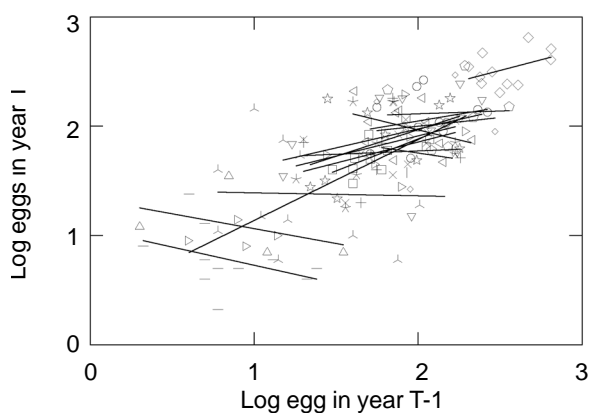


Figure 5. Relationship between egg number index (spawn clump numbers) in consecutive years. Values are scaled by a 10 log transformation. Each point represents data from one pond and one year. Different ponds have different symbols. The lines are within pond linear regressions.

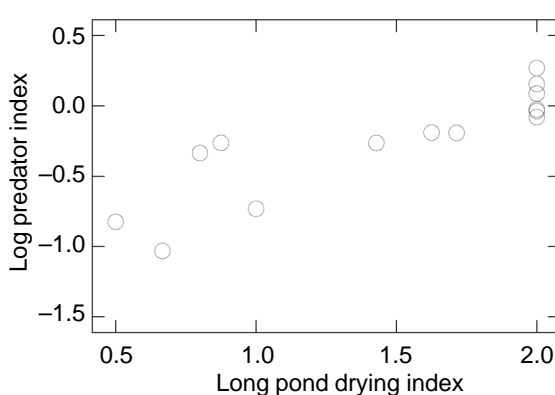


Figure 7. Relationship between predator presence and pond permanency. Each pond is represented by the mean value for all years. Permanent ponds have a mean drying index of 2, lower values represent degrees of pond drying in temporary ponds. The predator index is the 10 log of average number of predator individuals present.

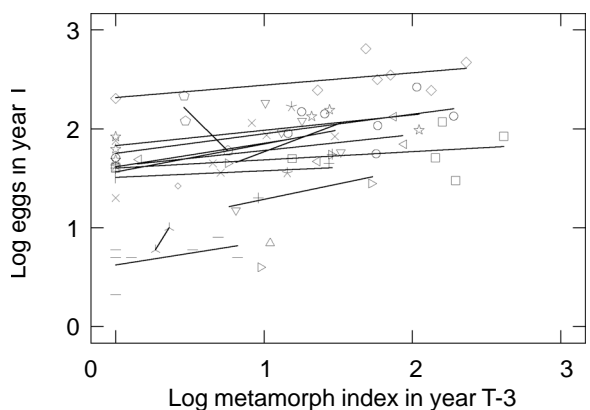


Figure 6. Relationship between the metamorph index and the eggs number index (= spawn clump numbers) 3 years later. Values are scaled by a 10 log transformation. Each point represents data from one pond and one year. Different ponds have different symbols. The lines are within pond linear regressions.

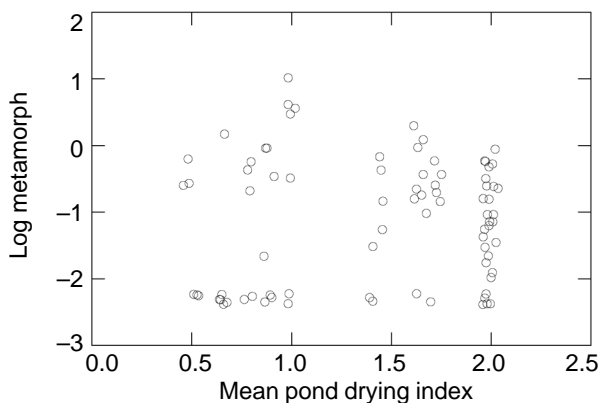


Figure 8. Effect of pond permanency on tadpole survival. Each symbol is based on one pond and one year. Drying index is the mean value for each pond. Metamorph survival is measured separately for each year. Survival is 10 log transformed and the value 0.005 represent no survival. Symbols are dislocated by a small random error to avoid overlap on the $y = -2.30$ (= minimum survival) and $x = 2$ lines.

Table 3. Frequency and distribution pattern of predators. Mean # is the mean number of predators per netting unit (a stroke covering 1 m²). Correlation is the Spearman correlation co-efficient for a comparison of pond-wise mean number versus the ponds mean drying index. This index is 0 if a pond dried before metamorphosis in a year, 1 if it dried during metamorphosis and 2 if it did not dry, or did so after completed metamorphosis in a year. The limit for a significant correlation at the 0.05 level is 0.62. However, if one corrects for multiple tests (in this case 12), the corresponding r_s value is 0.95.

	Mean #	Correlation
Larval Anisopteran	0.154	0.73
Adult <i>Dytiscus</i> sp.	0.074	0.66
Larval <i>Dytiscus</i> sp.	0.223	-0.38
Smaller Dytiscidae	0.037	0.09
<i>Corixa</i> sp.	0.085	0.89
<i>Nepa cinerea</i>	0.014	0.05
<i>Ranatra linearis</i>	0.001	0.26
<i>Ilyocoris cimicoides</i>	0.018	0.42
<i>Haemopsis sanguisuga</i>	0.054	-0.36
Adult <i>Gasterosteus aculeatus</i>	0.067	-0.06
Adult <i>Triturus cristatus</i>	0.017	0.20
Adult <i>Triturus vulgaris</i>	0.084	0.36

dency (Table 3). The only exceptions were *Dytiscus* larvae and leeches *Haemopsis sanguisuga* that were more common in temporary than in permanent ponds.

In temporary ponds there was a higher variation in metamorph survival; In wet years survival was better than in the average permanent pond while in the dry years there was no survival (Figure 8.). The effect of drying type on the variance in metamorph survival was significant ($N = 15$, Spearman $r_s = 0.666$, $P < 0.05$). However, there was no effect of pond drying on variation in number of spawn clumps laid in spring (Spearman $N = 16$, $r_s = 0.075$, $P > 0.10$).

Discussion

Tadpole density and metamorph indices

The fact that there was a strong correlation between the indices of tadpoles and metamorphs is not surprising, because this result is based on non-drying ponds only and the tadpole count was performed when the tadpoles were close to metamorphosis. Some inter-year variation in the correlation could be due to the fact that the tadpoles were censused on fixed (or almost fixed) dates, while the metamorphs were censused at different times, metamorphosis taking place later in cold years. This could manifest as a year effect. This was however not quite significant. Essentially, both measures, tadpole density and metamorph index, measure the same thing, namely tadpole survival, and

the strong correlation shows that some confidence can be put in these measures, despite the large variation expected from the two methods. This also means that the analyses of tadpole survival and metamorphs survival from hatched eggs to the respective stage, should be considered two parallel analyses of tadpole survival that may or may not support each other.

Density effects on tadpoles and metamorph survival

The overall correlation between spawn clumps and tadpole numbers is of course largely an effect of a large variation in egg numbers among ponds, which is partly related to pond area. In the present set of ponds there are more breeding frogs in the large ponds than in the small ponds. The fact that there is also a within pond effect of spawn clump number, shows that there is no strong density dependent effect on tadpole survival, nor a large random variation. Accordingly, no direct effect of original (eggs and thus newly hatched tadpoles) density could be detected. A similar, direct, correlation between egg number and metamorph output was also found for *Bufo calamita* by Beebee et al. (1996).

There was no suggestion of density effects on tadpole or metamorph survival. Within ponds, survival was as good in high density years as it was in low density years. Comparing the different ponds, there was on the contrary, higher survival in high density ponds. One possible interpretation of this is that frogs favoured high survival ponds (leading to high spawn clump density) for breeding. Brönmark & Edenharn (1994) found in a field survey that *Hyla arborea* avoid ponds with fish (which feed on the tadpoles) for breeding and Hopey & Petranka (1994) found in an experiment that *Rana sylvatica* avoid breeding in ponds with predatory fish. However, a similar experiment by Laurila & Aho (1997) failed to find such an effect. It does not seem improbable that such an active choice is the cause of the pattern found in this study. As an alternative, the high survival could be the cause of the high density.

Some studies have, in contrast to this one, demonstrated density dependent effects on tadpole survival (Smith 1983; Berven 1990; Pechman 1994). The first study implied competition of food as the proximate factor mediating the density effect. In the present study area, it has been demonstrated (Loman 2001a), that tadpole grazing does affect periphytic algae, which gives a potential for resource competition. In this study, it was not apparent that this effected survival. However, another study in the same area indicated that performance (growth and development) but not survival of *Rana arvalis* tadpoles was affected by density (Loman 2001b).

The significant interaction between pond and egg density effects on tadpole number (Figure 2) implies that it is important to attempt a characterisation of the four ponds that did not fit the general pattern; but surprisingly had a (slight) decrease in tadpole density with increasing number of egg laid in the pond. Intraspecific competition could, hypothetically, affect the pattern. This would mean that high density ponds, with many eggs per pond area, suffer higher mortality and a weaker dependency of tadpoles from egg numbers. However, this was not supported because, though far from significant, the present data showed actually the opposite tendency. There is also a methodological effect that may contribute. Low egg (and thus tadpole) density ponds yielded small sample sizes for the computation of tadpole density. This means that data from these ponds has a higher variation than that from high density ponds and any real patterns in these ponds may disappear because of low power. In summary, the present data does not allow any conclusions to be drawn from the variation in slope. Rather, it supports the not too surprising conclusion that years with high number of eggs result in years with high numbers of tadpoles, if pond drying effects are disregarded. Although the result is not surprising, it is important. It shows that, in these ponds, an increase in the number of eggs laid would have led to an increase in tadpoles and metamorphs. At least at present population densities, ponds do not seem to be limiting for these populations.

Predation effects on tadpoles and metamorph survival

It is found that part of the variation in tadpole survival can be explained by predator presence. In years when there were many predators in a pond, survival was less. Several other studies have shown that predation is an important source of mortality for tadpoles in the field (Laurila & Aho 1997; Laurila 1998; Williamson & Bull 1999; Nyström et al. 2001). Some find that predation is particularly important for young tadpoles (Licht 1974; Cecil & Just 1979; Denton & Beebee 1997). This is also supported by the behaviour of tadpoles in a laboratory study (Van Buskirk & Relyea 1998). However, there is no direct evidence that this mortality is density dependent.

If predation is density dependent, this would reduce the increase in tadpoles with increasing number of eggs in high predator ponds. This could have explained the lack of a correlation between eggs and tadpoles found for some ponds (the four negative slopes seen in Figure 2). There was indeed a tendency toward this, as these four ponds had high predator indices, though the pattern was not significant.

Predation and density can also have indirect effects on survival. In a laboratory study with caged predators

(Van Buskirk 2000), tadpoles of several species responded morphologically and behaviourally to the presence of predators. This negatively affected their growth rate. Morey & Reznick (2001) raised tadpoles at different densities. Crowded tadpoles grew to smaller sizes and had limited survival, when later released in the field.

Effect of pond drying on population dynamics

Breeding in temperate ponds has both advantages and disadvantages. The disadvantage is of course that early drying means the risk of tadpole loss before metamorphosis in dry years. This has indeed been shown as an important factor of mortality for tadpoles of several species (Beebee & Beebee 1978; Berven 1995; Rowe & Dunson 1995; Skelly 1996; Denver 1997; Laurila & Kujasalo 1999; Loman 2002). The advantage is that some potential tadpole predators, including most fish, can not survive in a pond that occasionally dries (Wiggins et al. 1980; Smith 1983; Wellborn et al. 1996; Skelly 1996; Barandun & Reyer 1997). The present study confirmed this pattern, there were less predators in temporary than in permanent ponds. This is probably the reason why there was the highest variation in survival found in temporary ponds. Although many years produced few or no recruits (due to pond drying), other years showed examples of higher survival than that recorded in the permanent ponds.

Between year population dynamics

Population size was significantly affected by (a) the number of recruits two and three years before. This is consistent with the picture of female common frogs reproducing for the first time at two or three years of age and thereafter yearly (Loman 1978; Gibbons & McCarthy 1986; Ryser 1988; Augert & Joly 1993; Miaud et al. 1999). (b) In this study there was also a correlation between number of eggs (i.e. adult population) in consecutive years. This shows that adult survival is large enough to smooth, potentially large, population fluctuations caused by the variation in metamorphosis success. If most females only bred once, the large variation in the number of metamorphs, that were especially evident in temporary ponds, would lead to large variations in adult populations. This number depends on the number of metamorphs two or three years previous and on juvenile survival. However, published information on adult survival (Loman 1984; Gibbons & McCarthy 1984; Elmberg 1990) suggests an adult female yearly survival of at least 25%. In addition, the study ponds were not isolated but dispersal from neighbouring ponds could reduce the effect of variation in number of metamorphs. In particular, the 4

ponds that most frequently dried early during summer had large permanent ponds with breeding frogs at distances of 200 m, 600 m, 400 m and 500 m. This may be well within the range of regular dispersal. This finding underlines the fact that ponds are not usually independent units (demes) for population dynamics in *Rana temporaria* and other species' of frogs (Pope et al. 2000, Marsh & Trenham 2001). (c) Significant year effects modified the effects of the adult population one year previous and metamorphs two years previous. These year effects could represent climatic effects on survival but in principle also climatic effects on the proportion of females breeding in any given year. Climatic effects could also operate by delaying age of first breeding for females, following a summer with poor feeding conditions.

In summary, three factors were to some extent present and of importance for yearly variation in population numbers: number of metamorphs two and three years previous, number of adults in the previous year, and year specific (probably climatic) factors. Beebee et al. (1996) found that metamorph success was the most important factor affecting adult population size in *Bufo calamita*. There was no evidence that metamorph production was density dependent. Also Berven (1990, 1995) found that variation in adult *Rana sylvatica* population was largely due to variation in metamorph production. However, he found density dependence effects on metamorph and juvenile survival. Williamson & Bull (1999) also state that the aquatic phase is the key phase in the dynamics of this species. The studies of these three species were all based on populations living in temporary ponds that occasionally dried, leaving little or no, surviving metamorphs. Effects of adult density have been found by Reading & Clarke (1995) and in the time series analysis by Meyer et al. (1998). Others have also found effects on yearly variation in weather on aspects of adult frog population dynamics (Berven 1990; Kutenkov 1995; Reading & Clarke 1995; Stewart 1995; Woolbright 1996; Kutenkov & Mosiyash 2000).

This study shows that the production of metamorphs is effected by variation among ponds and years, in predator number and pond hydroperiod, but that density dependent effects are of little importance. The number of metamorphs does in turn affect the size of the breeding populations two and three years later, but the effect is strongly levelled out by adult survival and possibly inter pond dispersal.

Implications for frog conservation

Declines of amphibian populations have recently attracted a considerable interest. Many causes for such a trend have been suggested, alone or in various combi-

nations; global climate changes (Pounds 2001), epizootics (Berger et al. 1998), UV-radiation (Blaustein et al. 1994). One factor that has not attracted as much attention but probably is as important for anurans (Delis et al. 1996) as for most other groups of animal is habitat alterations (Tilman et al. 2001). In the present study area, populations of *R. temporaria* are not generally declining (Loman 2001c). However, locally, populations are threatened by habitat changes, in particular draining of ponds and moist areas. For this reason, habitat protection and restorations may be required in this as well as in many other areas.

In this context there are two lessons to be drawn from the study. First, there does not appear to be strong density effects during the aquatic stage of this species. This suggests that, provided suitable ponds are present, more efforts should be directed to manage the terrestrial habitat of frogs, rather than to enlarge existing ponds or supplement them with more ponds in the same general area. Of course, an area devoid of suitable breeding ponds would benefit from pond management. Also, it stresses the importance of temporary ponds, viable populations may subsist even if a pond frequently dries before metamorphosis. These types of ponds are often found in areas subject to draining and may be overlooked when the value of an area for conservation is assessed (Collinson et al. 1995; Williams 1997). Active pond management often uses such areas for the creation of new ponds, aimed at supporting frogs. This may be sometimes lead to misdirected efforts, or even be counter productive.

Acknowledgements: Many people have assisted in the field over the years. For this I would like to thank Björn Lardner, Ingegärd Ljungblom, Jonatan Loman, Torkel Loman, Gunilla Lundh, Elsa Månsson, Håkan Sandsten, Herman van Steenwijk, and Ralph Tramontano. Björn Lardner's comments greatly improved the text. The work has been financed by Swedish Council for Forestry and Agricultural Research.

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Received 30.11.01

Accepted 24.04.02