Wetlands Ecology and Management **9:** 135–139, 2001.

Effects of tadpole grazing on periphytic algae in ponds

Jon Loman[1]
Dept. Animal Ecology, Ecology Building, Lund University, SE-223 62 Lund, Sweden;
E-mail: Jon.loman@zooekol.lu.se

Received 10 April 1999; accepted in revised form 22 December 1999

Key words: Anura, feeding, ponds, Pulmonata, tadpoles, snails

Abstract

Tadpole impact on periphytic algae was estimated with an exclosure experiment in the field. Algae growth on control (exposed) and experimental (netted-in) perspex plates was measured in 12 ponds in 1991 and 8 in 1993. An index of snail (*Lymnea* and *Planorbis*) presence in the ponds was used to correct their effect. Grazing pressure (difference in amount of algae between control and experimental plates) differed between ponds. The difference was correlated to amount of *Rana* tadpoles present in the pond. At the higher densities of tadpoles observed in the study ponds, the algae standing crop on exposed plates was about 50–75% of that on netted-in plates. These result demonstrate that there is potential for effects of exploitation competition in ponds with a high tadpole density.

Introduction

Most temperate *Rana* tadpoles are generalistic algae feeders (Savage, 1951; Seale, 1980). Important food categories include filamentous green algae (Dickman, 1968), epiphytic diatoms (Kupferberg, 1997), detritus (including decomposed higher plants) and various algae (Jenssen, 1967).

Grazing by tadpoles potentially reduces algae biomass (Brönmark et al., 1991). A review shows that, generalizing over all grazers, periphyton removal rate increases with increased grazer biomass (Cattaneo and Mousseau, 1995). However, the effects of grazing by tadpoles and other epiphytic grazers on the algae community can be very complex. By removing epiphyton growing on filamentous algae or macrophytes, the latter are favored by tadpoles (Kupferberg, 1997) or invertebrates (Dodds, 1991; Underwood, 1991). Also, algae may benefit from increased nutrient levels caused by grazing tadpoles (Osborne and McLachlan, 1985) or invertebrates (Gresens, 1995).

So, the effect of tadpoles on algae is likely to be very variable. The impact is important also for the tadpoles themselves. If there is no effect, tadpoles in the specific site are not likely to be resource limited. On the other hand, if one finds an effect of tadpole grazing on the algae flora in a pond, there is a possibility that tadpoles are resource regulated. Indeed, several studies have shown an effect of algae abundance on tadpole growth rate (Johnson, 1991; Leips and Travis, 1994). The present study searches for effects of tadpoles on the periphytic algae in south Swedish ponds, inhabited by *Rana arvalis* and *R. temporaria* tadpoles. The effect of grazing was measured by an exclosure experiment. The growth of algae in the field was monitored both on exposed surfaces and on surfaces where tadpoles and other grazers were excluded. The only other group of grazers commonly found in the study ponds was snails. Because they were similar in size to tadpoles, their effect could not be separated experimentally. Instead, their abundance was measured and the effect of tadpole density on observed grazing impact was statistically corrected for snail abundance.

Material and methods

Algae growth chamber

Test chambers were made from perspex. They were made up of a ‘half-pipe’ shaped roof and a flat floor plate, kept together with rubber bands. The floor area was 80 $\times$ 80 mm. The ends of the chambers were 'extended' by 5 mm thick profiles, also kept in place with rubber band. The control (open) chambers had no more elements and were thus open in both ends. The experimental (exclosure) chambers had a piece of 2mm plastic mesh fixed between the end profile and the main chamber. Thus nothing wider than 2 mm could enter the chamber. This excluded tadpoles above about 1 week of age. Only the up (inner) side of the flat, bottom, plate was used as substratum for actually measuring algae growth.

Study area

The study ponds were situated in the central and southwestern part of Skåne, the southernmost province of Sweden. Twelve ponds were used in 1991 and eight ponds in 1993. Out of these, six ponds were used in both years (Figure 1). In all ponds *Rana* tadpoles (*Rana arvalis* and/or *R. temporaria*), but no other anurans, were known to be present. Eggs of these frogs hatched during the latter half of April and tadpoles metamorphosed from the beginning of June. The size of the ponds varied between 200 and 2500 m^2. Most ponds (AD17, AD18, HP27, M3, M4, R3, R4, and R5) were located in grazed meadows. Three were located in moist forests (AP4, AP5, and HP25). In all these, algae grew on submerged plants. One pond (HL8) was situated in a cropped field. This had, in addition to submerged plants, plenty of stones as substrate for algae. Most ponds were free from fish but Stickelback (*Pungitius pungitius*) was know to be present in ponds AD17 and AP4 and Carussian carp (*Carassius carassius*) in pond R5.

Procedures

The test chambers were placed in pairs consisting of one control and one experimental treatment, located about 10 cm from each other. They were placed on the pond bottom at a depth of about 15 cm. If necessary, the chambers were moved to deeper water if the pond's water level dropped during the course of the study. In each pond, there were four (in one case eight) such sites. Some chambers became useless because they were stepped on by cows or because water level dropped faster than anticipated, leaving them dry on the shore.

In 1991, the chambers were put out on May 14th and 15th and recovered on June 11th. In 1993 they were put out on May 13h and 14th and recovered on May 26th. The period of growth was shorter in 1993 because this spring was very warm and some of the experimental ponds begun to dry up completely.

Once per week the chambers were temporarily disassembled and all algae growing on the roof was removed to avoid shading. After the experiment, the chambers were disassembled and the floor plates gently rinsed in water to remove loose sediment. Also, all algae on the out (down) side of the floor plates was removed. They were then allowed to dry completely. After that the plates were weighed, all algae on the top side was removed and the plate weighed again. This gave a measure of the dry weight of the algae growing on the floor inside.

Measures

For the first analysis, I used actual dry weight of algae on the individual perspex plates. For subsequent analyses I computed, for each pond, the average amount of algae present on plates in control (open to grazing) and experimental (grazing not possible) chambers, respectively. The former value divided by the latter was computed and termed 'Grazing quotient'. I also computed the difference between the values, 'Grazed amount'. This procedure, rather than computing the quotient and amount separately for each site (within a pond), was adopted because it used more data. Several chambers were lost by being stepped on by cattle and the alternative procedure had required dropping of both chambers at a site if one was destroyed. Also, there was no significant effect of site (nested under pond) on amount of algae ($p = 0.14$, full details for this ANOVA given in the first section of the results).

Grazer counts

Tadpoles and snails were captured with a scraper net. In each pond, samples were taken twice each year, once around May 20th and once around June 5th. The average of these two recordings was used in the analyses. Each sample consisted of 5–20 strokes (depending on pond size) with the net, each covering 1 m^2 of the bottom (actually, depending on pond topography, each stroke sometimes consisted of several substrokes). The number of tadpoles and snails respectively per stroke was used as an index of their density in the pond. This maximum number of tadpoles recorded for any pond in the study was 214/m^2 (or 2.95 g m^{-2} dry weight). In most ponds, the density was one or two orders of magnitude less (Figure 2). Before analysis, numbers were $\log_{10}$ transformed. The $\log_{10}$ value of empty samples was set to the lowest

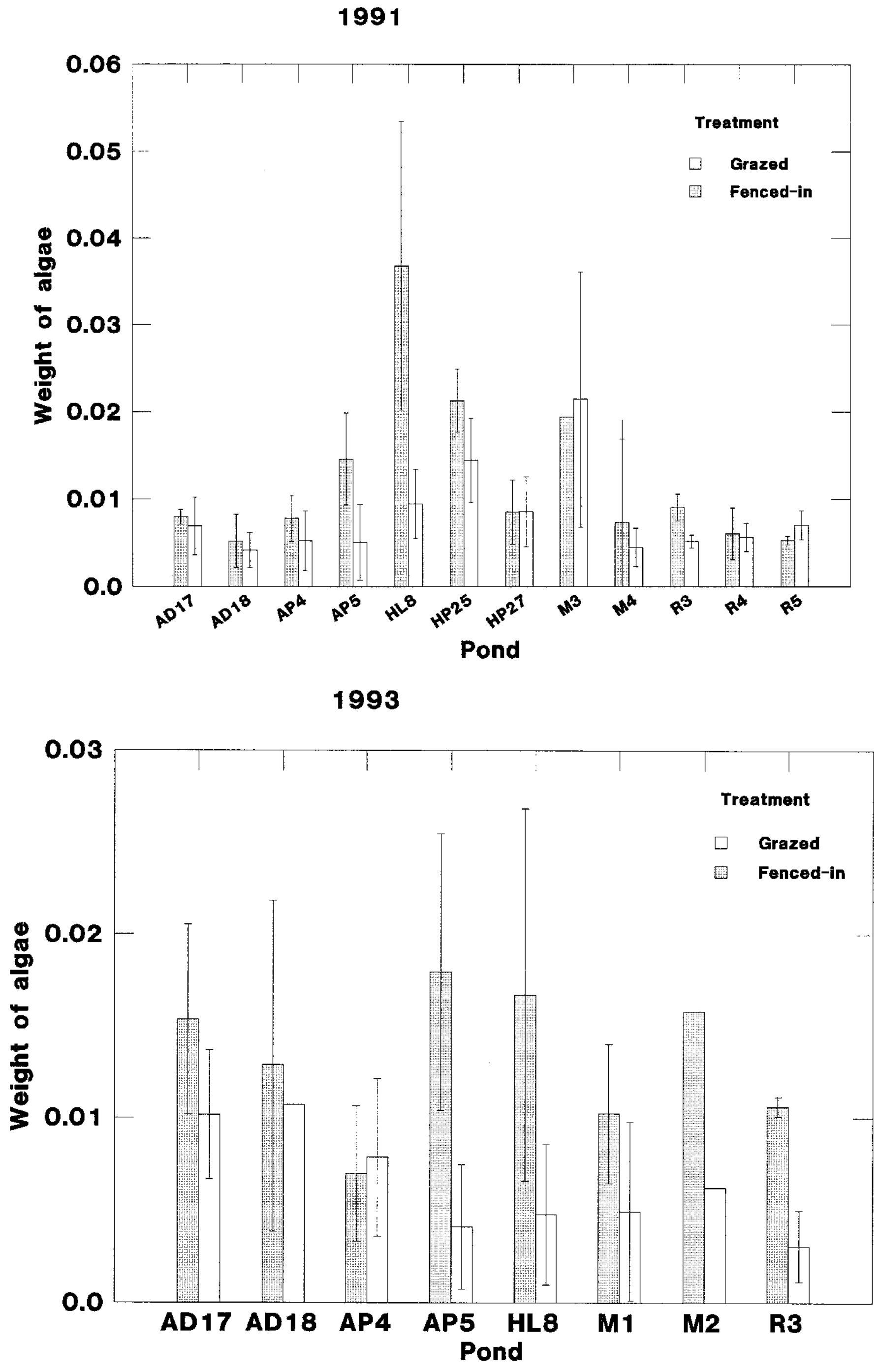

Figure 1. Amount of epiphytic algae (grammes per 64 cm2 plate) present after exposure in the field. Filled bars represent plates excluded from grazing while open bars represent plates that were open to grazers. Error bars indicate S.E.

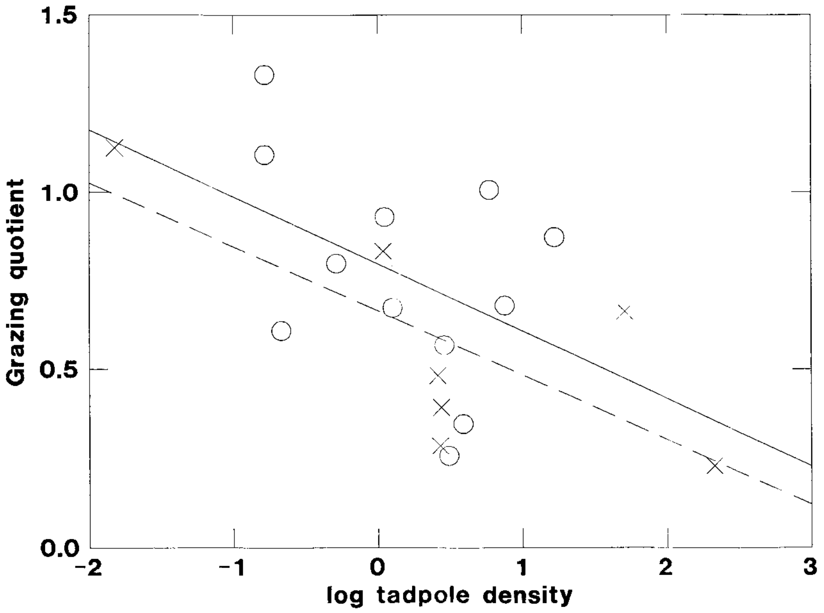

Figure 2. Grazing effect (growth on exposed plates divided by growth on caged plates) related to density of *Rana* tadpoles ($\log_{10}$ tadpole individuals m^{-2}). 1991 data shown by circles and the filled line, 1993 data by crosses and the dashed line.

$\log_{10}$ value for ponds with tadpoles present minus one. Only snails above 5 mm in maximum shell size were counted. This represented a size gap, separating juveniles from older. The snail individuals were distributed thus: *Lymnea stagnalis* 3.3%, L. *peregra* 26.5%, *Planorbis cornutus* 0.1%, and P. *planorbis* 70.0%. The two *Rana* species were not separated in these samples. The proportion of *Rana arvalis* varied between 0% and 90% over the different ponds (pers. obs.).

Results

The average amount of algae was, in most ponds, less in the open (control) chambers than in experimental (covered) (Figure 1). Actually, there was a significant effect (tested by a 4-way ANOVA) on amount of algae present from pond (d.f. = 13: 76, F = 1.96, $p = 0.037$) and treatment (open vs. covered, d.f. = 1: 76, F = 6.61, $p = 0.012$). There was also a significant interaction between pond and treatment, i.e. the effect of the treatment was more drastic in some ponds than in others (d.f. = 13: 76, f = 2.40, $p = 0.009$). Within pond, the effect of site was not significant (nested under pond, d.f. = 42, F = 1.33, $p = 0.14$). The last factor of this ANOVA was year (d.f. = 1: 76, F = 2.43, $p = 0.123$). This was included to correct for year differences in weather and exposure time.

There was a significant negative correlation between tadpole density and grazing quotient (each pond and year combination used as one data point, tests use Pearson's correlation coefficients) (N = 20, r = –0.58, $p = 0.009$) (Figure 2) while the correlation between tadpole density and grazed amount was not quite significant (N = 20, r = 0.45, $p = 0.051$).

The effect of tadpole density on the grazing quotient, while controlling for year effects and snail density, was tested with a 3-way ANCOVA. This showed that density of tadpoles had a significant effect on grazing (d.f. = 1: 15, F = 5.26, $p = 0.037$). There were neither an effect from snail density (d.f. = 1: 15, F = 0.040, $p = 0.54$) nor from year (d.f. = 15, F = 1.32, $p = 0.27$). In these tests, 2-way interactions (of tadpole and snail density with year) were not significant and removed from final analysis.

Discussion

The treatment, netting-in the test plates, obviously did affect algal growth. This could be, or could not be, due to the exclusion of grazers. The alternative explanation to a grazer effect could be some effect of difference in water quality caused by the net. However, the interaction between treatment and pond supports (but does not prove) the grazing hypothesis. If this hypothesis is acceptable, then ponds with high tadpole densities should have a high difference in growth between treated and non-treated plates, producing an interaction, which was found. Even stronger support for this hypothesis comes from the correlation between tadpole density and effect of the experimental treatment and from the outcome of the ANCOVA.

Apart from variation in grazer densities, there were obviously other sources to variation in algal growth. The nature of these is outside the scope of this study. It is however noteworthy that the pond situated in cropped field (HL8) in both years had among the highest growth of algae (Figure 1).

Consequences of tadpole grazing

So, what interesting things do these results tell us? It is known that both snails and tadpoles graze algae (Jenssen, 1967; Dickman, 1968; Brönmark et al., 1991; Kupferberg, 1997). and it is not surprising that more tadpoles will graze a higher fraction than few tadpoles. However, something that would be interesting is evidence that grazing is potentially quantitatively important, structuring the algae community and/or affecting the feeding conditions of the tadpole population itself. Food rations have been shown to affect tadpole growth rate in *Rana sylvatica* (which has a natural history that similar to that of *R. arvalis*) (Wilbur, 1977; Murray, 1990) and in other taxa e.g., *Scaphiopus couchii* (Newman, 1994). Also, in an experiment directly manipulating tadpole densities in the field, intraspecific effects of density on growth rate were found for *R. arvalis* at high densities (Loman, 1997).

Because the negative slope in Figure 2 was significant, it is possible to discuss also the quantitative effects found in this study. It does indeed seem that at high, but still naturally occurring, tadpole densities, a reduction of algae growth during the first half of tadpole development to about 25 to 50% of non-grazed density is likely in this area. This was recorded in this study when the experiments concluded with tadpoles that had reached about three quarter (1991) or half (1993) of their full aquatic development time. Later, the larger tadpoles may cause even stronger grazing effects. Alternatively, increased algae growth may take place as the season progresses, reducing the effects of tadpoles (and snails) on algae and also the potential for a feed back on the grazer populations. Only further experiment can show what effect this has on tadpole growth. However, this study suggests that there is some potential for intraspecific competition in natural high density ponds while this is not likely in ponds with natural low tadpole densities.

Acknowledgements

This work was supported by the Swedish Council for Forestry and Agricultural Research. B. Lardner and H. van Steenwijk helped with the field work. Comments from B. Enoksson, B. Lardner and T. Madsen improved the presentation.

References

Brönmark, C., Rundle, S.D. and Erlandsson, A. 1991. Interactions between freshwater snails and tadpoles: competition and facilitation. Oecologia 87: 8–18.

Cattaneo A. and Mousseau, B. 1995. Empirical analysis of the removal rate of periphyton by grazers. Oecologia 103: 249–254.

Dickman, M. 1968. The effect of grazing by tadpoles on the structure of a periphyton community. Ecol. 49: 1188–1190.

Dodds, W.K. 1991. Community interactions between the filamentous alga *Cladophora glomerata* (L.) Kuetzing, its epiphytes, and epiphytic grazers. Oecologia 85: 572–580.

Gresens S.E. 1995. Grazer diversity, competition and the response of the periphyton community. Oikos 73: 336–346.

Jenssen, T.A. 1967. Food habits of the green frog, *Rana* clamitans, before and during metamorphosis. Copeia 1967: 214–18.

Johnson, L.M. 1991. Growth and development of larval northern cricket frogs (Acris crepitans) in relation to phytoplankton abundance). Freshw. Biol. 25: 51–5).

Kupferberg, S. 1997. Facilitation of periphyton production by tadpole grazing: functional differences between species. Freshw. Biol. 37: 427–439.

Leips, J. and Travis, J. 1994. Metamorphic responses to changing food levels in two species of hylid frogs. Ecol. 75: 1345–1356.

Loman, J. 1997. Natural density regulation in tadpoles of the moor frog *Rana* arvalis – preliminary report of a field experiment. Herp. Bonnensis 1997: 247–255.

Murray, D.L. 1990. The effects of food and density on growth and metamorphosis in larval wood frogs (*Rana* sylvatica) from central Labrador. Can. J. Zool. 68: 1221–1226.

Newman, R.A. 1994. Effects of changing density and food level on metamorphosis of a desert amphibian, Scaphiopus couchii. Ecol. 75: 1085–1096.

Osborne, P.L. and McLachlan, A.J. 1985. The effect of tadpoles on algal growth in temporary, rain-filled rock pools. Freshw. Biol. 15: 77–87.

Savage, R.M. 1952. Ecological, physiological and anatomical observations on some species of anuran tadpoles. Proc. Zool. Soc. 122: 467–514.

Seale, D. 1980. Influence of amphibian larvae on primary production, nutrient flux, and competition in a pond ecosystem. Ecol. 61: 1531–1550.

Underwood, G.J.C. 1991. Growth enhancement of the macrophyte Ceratophyllum demersum in the presence of the snail Planorbis planorbis: the effect of grazing and chemical conditioning. Freshw. Biol. 26: 325–334.

Wilbur, H.M. 1977. Interactions of food level and population density in *Rana* sylvatica. Ecol. 58: 206–209.