HERPETOLOGICAL JOURNAL, Vol. 7, pp. 149-154 (1997)

MICROENVIRONMENTAL EFFECTS ON COMPETITION BETWEEN *RANA* AND *BUFO* LARVAE, AND ON THE ABUNDANCE OF *PROTOTHECA RICHARDSI*, IN SMALL FISH-PONDS

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Previous laboratory and replicated pond experiments have implicated *Prototheca richardsi*, a unicellular alga, in interference competition within larval anuran assemblages. We investigated the extent of interspecific competition between *Rana temporaria* and *Bufo bufo* larvae, and the occurrence of *P. richardsi*, in small fish-ponds where initial tadpole densities were high. Mortality of both *R. temporaria* and *B. bufo* larvae was high during the early stages of development, and interspecific competition was negligible in these ponds and in mesh cages suspended in them. However, growth of *B. bufo* larvae was reduced when they were raised with *R. temporaria* larvae at natural densities in plastic cages within the ponds. *P. richardsi* was positively associated with the plastic cage treatments, but was much less frequent in the ponds outside or in the mesh cage treatments. Predation appears to be a much more important structuring force than either resource competition or *Prototheca*-mediated interference competition in the anuran communities inhabiting these fish-ponds.

INTRODUCTION

Assemblages of larval anurans offer an ideal opportunity to study competitive interactions between species with high degrees of niche overlap. Inter- and intra-specific competition have been demonstrated between anuran larvae under both laboratory and field conditions (e.g. Heusser, 1972; Dash & Hota, 1980; Morin, 1981, 1983; Griffiths, 1991). This competition may be mediated by both resource and interference mechanisms (e.g. Griffiths, Denton & Wong, 1993; Beebee, 1996). Over the past 40 years microscopic organisms have been implicated as mediators of interference competition in a number of anuran species (e.g. Richards, 1958; 1962; Steinwascher, 1979; Petranka, 1989). Beebee (1991) demonstrated that a species of unpigmented unicellular alga, *Prototheca richardsi*, mediated growth inhibition of anuran larvae under laboratory conditions. Growth inhibition was also induced in replicated artificial ponds by rearing small *Bufo* tadpoles in water containing *Rana temporaria* faeces (Griffiths, Edgar & Wong, 1991), again implicating *P. richardsi* in interference competition between anuran larvae kept at moderate densities. There is some doubt, nevertheless, as to whether *Prototheca*-mediated competition is significant in the field and Petranka (1995) and Biesterfeldt, Petranka & Sherbondy (1993) provided evidence that although *Prototheca* cells were present in the natural breeding habitat of *R. sylvatica*, they were not involved in growth inhibition.

The two widespread British anurans *R. temporaria* and *Bufo bufo* exhibit a high degree of sympatry in their geographical distributions (Arnold, 1995) and frequently breed in the same water bodies. However, the common toad *B. bufo* generally spawns days or weeks later than the common frog *R. temporaria,* and the former species may therefore be competitively disadvantaged during larval development. In southeast England, small garden fish-ponds are important breeding sites for both species (Beebee, 1979). Population densities in these ponds are often higher than in their rural counterparts due to the inherent limitations in size of garden pools. These ponds thus provide interesting sites for examining interspecific competition between *R. temporaria* and *B. bufo* at high but natural breeding densities. This study was designed to assess the extent of any such competition and the relative strengths of resource and interference (*P. richardsi*-mediated) components in garden fish-ponds.

MATERIALS AND METHODS

STUDY PONDS

Three garden ponds (S, C and R) with naturally-occurring populations of *R. temporaria* and *B. bufo* were chosen as replicates from a data bank of such ponds in the Brighton (Sussex,UK) area. All ponds contained substantial numbers of goldfish (*Carassius auratus*) and similar percentages of submergent and emergent vegetation, but differed in size and depth. Pond R had a perimeter of 22.6 m, mean depth of 10 cm and held about 1770 litres of water; corresponding values for pond C were 9.7 m, 30 cm and 700 litres, and for pond S, 7.4 m, 30 cm and 410 litres.

TADPOLE DENSITY, SURVIVAL AND GROWTH

Spawn clumps of *R. temporaria* and strings of *B. bufo* were counted in each pond within one week of oviposition. The latter species spawned at least two weeks after the former in ponds R and C, but some four weeks after *R. temporaria* in pond S. *R. temporaria* egg numbers were estimated by multiplying the number of spawn clumps by 1300 (Cooke, 1975*a*). *Bufo bufo* egg numbers were calculated by counting the average

number of eggs present in 20 random 10 cm string sections and multiplying by the total estimated string length. Egg density was calculated by dividing total egg numbers by the volumes of the ponds to give an estimate of eggs/litre. Mark-recapture (Banks & Beebee, 1988) was carried out on *R. temporaria* tadpoles to estimate numbers in the ponds three and six weeks after hatching. When still present, *B. bufo* tadpole numbers were estimated by mark-recapture five weeks after hatching. In pond R, frog tadpole numbers were too high to mark-recapture on week three, so densities were estimated by counting tadpoles in five 50 cm x 50 cm areas of the pond and multiplying by the total area in which tadpoles were present.

Growth Condition Treatments

Six 10-litre cages were placed in each pond in February 1996, several weeks prior to the arrival of anurans. Each cage was an open-top nylon mesh cylinder which reached from the bottom of the pond to 5 cm above the surface. Three of these cages were placed directly in the pond, whilst the other three were first placed into plastic bags filled with pond water, also open-topped, and then into the pond. Water and organisms < 1mm^2 in cross section could pass between the main pond and the mesh cylinders, but plastic-coated cylinders were essentially impermeable to water and organisms from the rest of the pond. Each cage was filled with representative quantities of pond sediment and vegetation.

As soon as *R. temporaria* and *B. bufo* larvae were free-swimming in the study ponds, samples were placed at natural initial densities (as gauged from viable spawn estimates) into treatment cages. Each pond contained six cages, three of mesh only and three with plastic liners. Within each set of three, one cage had *R. temporaria* only, one *B. bufo* only, and one both species. Tadpole densities in the treatment cages were altered twice during the course of the experiment to mimic changes in natural densities in the main ponds, as gauged by later mark-recapture estimates. Each pond thus contained six different treatments, and each treatment was replicated three times (once in each of the three ponds). Replicates were in separate ponds to minimize individual pond effects in subsequent data analysis.

Free-swimming tadpoles in the main body of the pond acted as references against which treatments were compared. The treatments were divided into two groups: mesh cages and plastic cages. Each of these groups was divided into three treatments comprising one mixed species cage and two single species cages. The mixed-species cages contained larvae of both species at densities similar to those in the pond outside, and were thus controls for cage effects. The single-species cages each contained either *R. temporaria* or *B. bufo* larvae at their individual natural densities in the pond outside. Total tadpole densities in the single-species cages were therefore lower than those in the exterior pond. Mesh cage treatments allowed free interchange of micro-organisms and were designed to permit interference but not resource competition to persist at levels similar to those in the pond outside. Plastic cage treatments were designed to preclude microorganisms and thus to relieve both interference and resource competition. Tadpole growth rates were monitored by measuring total lengths (snout-tail tip) and body lengths (snout-vent) of 3-10 randomly-chosen individuals from the ponds ("free-swimmers") and from all treatment cages on a weekly basis.

Prototheca Titres

Faecal samples from two tadpoles from each treatment cage and from free-swimmers in the ponds were collected on a weekly basis from five weeks after hatching until metamorphosis. Each tadpole was placed in 20 ml water in a mesh cage for one hour, under field conditions. Faeces were then spun down in a bench centrifuge and re-suspended in 2 ml of water and shaken vigorously. 50 µl samples were placed on a haemocytometer slide and numbers of *Prototheca* cells counted under a phase contrast microscope (Beebee, 1991). The average number from each pair of tadpoles was used as the datum point.

Statistical Analysis

Statistical analysis was carried out on MINITAB Version 8.1 using an IBM PC. Mean tadpole length within a cage was treated as a datum point to ensure independence between measurements. The effects of treatment on body length were analysed by ANOVA (standard or repeated-measures with time and species composition as independent variables). The association of *Prototheca* with particular treatments was analysed using *G*-tests (Fowler & Cohen, 1990).

RESULTS

Survival in the Ponds

Mortality rates of both *R. temporaria* and *B. bufo* were high and six weeks after hatching less than 1% of *R. temporaria* larvae (relative to numbers of viable eggs) survived in all three ponds (Fig. 1). *B. bufo* bred two weeks later in pond S than in the other two ponds, while in pond R *B. bufo* larvae were not found more than three weeks after hatching. In pond C *B. bufo* survival was monitored successfully by mark-recapture and 5% of larvae survived five weeks after hatching. *R. temporaria* metamorphs were seen at all three ponds, but *B. bufo* metamorphs were only seen in pond C.

Treatment Effects

Starting densities of *R. temporaria* and *B. bufo* tadpoles within the experimental cages, calculated to reflect those in the ponds, ranged from 6-20 per litre. Tadpole survival was substantially higher in treatment cages than in the main body of the pond. Tadpole densi-

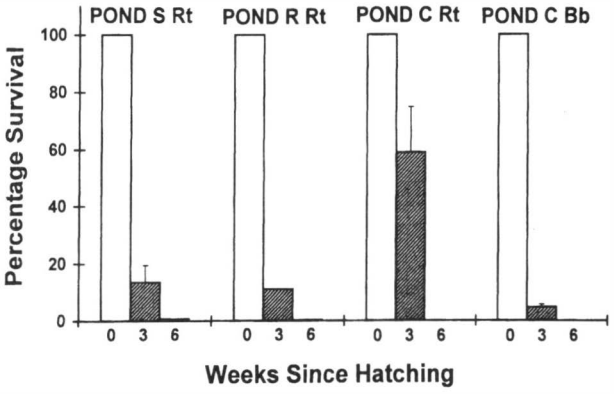

FIG.1 Percentage survival of *R. temporaria* (*Rt*) and *B. bufo* (*Bb*) larvae in all three study ponds. Estimates were made 3 weeks and 5/6 weeks after hatching, relative to numbers of viable eggs laid (week 0). Standard deviations of the estimates, where large enough are shown by error bars.

TABLE 1. Larval growth under different treatment regimes. *n*= no. treatment replicates (ponds or cages in which larvae were measured).

(A). SIZES (SNOUT-VENT LENGTHS) AT DAY 63 AFTER HATCH OF *R. TEMPORARIA* SPAWN

	Rana temporaria		*Bufo bufo*	
Treatment	*n*	Mean size mm (±SD)	*n*	Mean size mm (±SD)
Free swimming	3	12.8 ±1.3	2	10.9±1.3
In mesh cage	2	13.0 ±1.4	2	9.9±2.6
In plastic cage	3	12.3 ±0.9	2	10.3±1.1
In mesh + competitor	1	15.0	2	10.5±2.1
In plastic + competitor	2	12.7±0.9	2	9.6±2.0

(B). ANOVA OF GROWTH TO DAY 63 UNDER DIFFERENT TREATMENT REGIMES

B. bufo

Source:	DF	SS	MS	*F*	*P*
Factor	4	2.14	0.54	0.17	0.947
Error	6	19.10	3.18		
Total	10	21.25			

R. temporaria

Source:	DF	SS	MS	*F*	*P*
Factor	3	0.79	0.26	0.21	0.887
Error	6	7.54	1.26		
Total	9	8.32			

ties in treatment cages were therefore reduced at regular intervals to mimic densities in the main pond, and by the end of the experiment were at around 0.3 tadpoles per litre. Because free-swimming *B. bufo* larvae disappeared from pond R within 2-3 weeks of hatch, numbers of this species in cages in pond R were adjusted to densities comparable with those in pond C during the course of the experiment. Also, fish attacked the mesh cages in pond R and no useful data were obtained from this treatment group in that pond.

Tadpole size 63 days after the hatch of *R. temporaria* spawn is summarized in Table 1A for the various treatments. This was an arbitrary time point late during development and reflected cumulative growth rates. In almost all cases, data were available for only two out of the three replicates rather than the full set. This was due to various factors, including fish attack on the mesh cages in pond R and late spawning by *B. bufo* in pond S. ANOVA of the growth attained at day 63 indicated no gross differences between any of the treatments for either species (Table 1B), and little evidence of cage effects relative to free-swimming tadpoles. Nevertheless, there was an indication that *B. bufo* larvae in plastic cages with *R. temporaria* grew more slowly than under any other conditions. This was confirmed by closer analysis of growth rates in plastic cage treatments (Fig. 2). *B. bufo* alone in plastic cages (in ponds R and C) grew at rates indistinguishable from those free-swimming in pond C, the only pond in which *B. bufo* was available as a control from early enough in the experiment. However, *B. bufo* in plastic cages with *R. temporaria* grew consistently more slowly than those either caged alone or free-swimming. The effects of both time and competition (presence of *R. temporaria*) in plastic cages, but not of interactions between them, were highly significant as judged by repeated measures ANOVA (Table 2). No comparable effects on *R.*

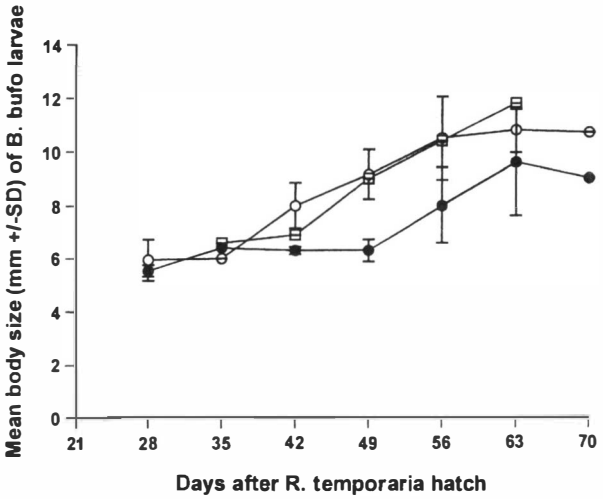

FIG 2. Growth rate of *B. bufo* larvae in the presence of and absence of *R temporaria* in closed plastic cages. Open squares, tadpoles free-swimming in pond C; open circles, averages of tadpoles caged alone in ponds R and C; filled circles, averages of tadpoles caged with R. temporaria in ponds R and C.

TABLE 2. Repeated-measures of ANOVA of growth of *B.bufo* larvae in a plastic cage

Source:	DF	SS	MS	*F*	*P*
Competition	1	14.42	14.42	20.50	<0.001
Time	5	67.34	13.47	19.15	<0.001
Comp.x time	5	4.04	0.81	1.15	0.388
Error	12	8.44	0.70		
Total	23	94.23			

temporaria larvae were observed in plastic cage treatments (data not shown).

PROTOTHECA TITRES

Table 3 shows the proportion of faecal samples containing *Prototheca* in each treatment group and the average numbers of *Prototheca* observed. Titres of *Prototheca,* when the organism was found, were comparable with those seen under laboratory conditions. The majority of free-swimming tadpoles and tadpoles in mesh cages had few or no protothecans in their faeces, but about one third of the samples examined from tadpoles in plastic cages contained *Prototheca.* This frequency was significantly higher than in mesh cages or the main ponds (*G*-test $P < 0.05$). There was, however, no specific association between growth inhibition and the occurrence of *Prototheca* in the plastic cage treatments. Growth-inhibited animals in mixed cages did not differ significantly in their production of *Prototheca* from the single species controls.

TABLE 3. *Prototheca* titres (*P.r.*) in faecal samples. *excluding one sample yielding $2.3x10^7$ protothecans / tadpole/hr. Figures in parentheses are proportions of total samples in each species-treatment in which protothecans were detected. Third column shows mean no. cells/tadpole/hr in positive samples.

Treatment/ Species	No. samples with *P.r.*	No. samples without *P.r.*	No. *P.r.*/ tadpole/hr
R. temporaria			
Free-swimming	1(0.09)	10	$1.0x10^5$
In mesh	0(0)	8	-
In plastic	4(0.31)	9	$2.7x10^5$
In mesh+*B. bufo*	1(0.14)	6	$2.2x10^5$
Plastic+*B. bufo*	5(0.38)	8	$4.7x10^6$ (*$1.8x10^5$)
Total	11(0.21)	41	$2.3x10^6$
B. bufo			
Free-swimming	0(0)	7	-
In mesh	0(0)	9	-
In plastic	4(0.33)	8	$3.4x10^5$
In mesh+*R. temporaria*	0(0)	7	-
Plastic+*R. temporaria*	5(0.45)	6	$4.0x10^5$
Total	9(0.20)	37	$3.5x10^5$

TABLE 4. Correlation coefficients of body versus total length for *R. temporaria* and *B. bufo* larvae before and after six weeks from hatching.

Conditions	*R. temp.* <wk. 6	*R.temp.* >wk. 6	*B.bufo* <wk. 6	*B. bufo* >wk. 6
In cages	0.946	0.917	0.932	0.957
Free-swimming	0.978	0.682	0.970	1.000

EVIDENCE OF LARVAL PREDATION IN THE PONDS

Vertebrate predator attacks frequently leave surviving tadpoles with mutilations, especially tail bites. Evidence of such attacks was apparent from examination of tadpoles within cages (protected from fish) and those free-swimming and exposed in the main ponds. Comparisons of tadpole total (including tail) and body lengths demonstrated that in the latter stages of development the correlation between these two measurements was weak for free-living *R. temporaria* but high for young larvae, caged animals of all ages, and for *B. bufo* under all conditions (Table 4). These data suggested that *R. temporaria* larvae were more prone to fish attack than were those of *B. bufo*, and that such predation occurred at a substantial level in all three ponds. The high length correlation in small *R. temporaria* larvae was unsurprising, because prior to the attainment of a size refuge predator attacks generally result in complete consumption rather than mutilation.

DISCUSSION

POPULATION DYNAMICS OF ANURAN LARVAE IN SMALL FISHPONDS

R. temporaria and *B. bufo* spawn densities were several-fold higher in small garden ponds than is normal in larger rural sites, including (for example) sand dune ponds (Banks & Beebee, 1987). Mortality of hatchlings was, however, very great. On average, less than 15% of *R. temporaria* survived for three weeks and by six weeks only 0.6-1.0% remained. Five percent of *B. bufo* hatchlings survived to five weeks post-hatching in the single pond where comparative measurement was possible. These survival rates were much lower than those found for *R. temporaria* and *B. bufo* in a sand dune ecosystem (Banks & Beebee, 1987), and low by comparison with most other studies of anuran development (reviewed in Davis, 1985). In all three garden ponds there were large numbers of vertebrate predators, predominantly goldfish (*Carassius auratus*). Carnivorous invertebrates, such as odonate larvae (*Anax* spp.) and backswimmers (*Notonecta* spp.) were also present. *R. temporaria* larvae are heavily predated by fish (e.g. Cooke, 1975*b*) and this probably explains the low numbers of *R. temporaria* surviving through to metamorphosis as well as the extensive tail damage seen in larger larvae. In the first few weeks after hatch-

ing, *R. temporaria* are suitable prey for gape-limited predators such as goldfish. Once the larvae are a few weeks old they become too large to be consumed by these predators, but many lose large sections of their tails instead (Cooke, 1974). *B. bufo* tadpoles are unpalatable to most (though not all) vertebrate predators (e.g. Reading, 1990) but are attacked by many invertebrates (Banks & Beebee, 1988). The widespread occurrence of predatory insects may explain the high mortality of *Bufo* larvae in garden ponds. Survival of both species was substantially higher in treatment cages than in the main ponds, implicating predation of some kind as the major cause of mortality.

Effect of Treatment on Tadpole Growth Rate and *Prototheca* Accumulation

Caged tadpoles in single-species treatments relieved from direct (resource) or direct and indirect (interference) competition from tadpoles free-swimming in the main pond grew at rates indistinguishable from those outside the cages. Interspecific competition between *R. temporaria* and *B. bufo* in these fish-ponds was therefore apparently insignificant in treatments that mimicked natural pond conditions and densities. This was presumably because of the rapid fall in tadpole numbers due to high levels of predation. Competition was however induced by placing tadpoles at natural densities in plastic cages with no flow-through of water. In this microenvironment *B. bufo* exhibited significant levels of growth inhibition in the presence of *R. temporaria.* There was however no evidence of intraspecific growth inhibition in *B. bufo* in plastic single species cages (relative to those outside or in mesh), and no effects on *R. temporaria* under any circumstances.

A number of experiments in the laboratory and using replicated ponds have implicated *P. richardsi* in the growth inhibition of competitively inferior anuran larvae (e.g. Richards, 1958; Beebee, 1991; Griffiths *et al.*, 1993). In this study, however, the relationship was unclear. Plastic cages were associated with growth inhibition and high *Prototheca* titres, but inhibited and uninhibited (single-species treatment) *B. bufo* larvae had equally high frequencies of *Prototheca* in their faeces. Plastic cages were designed to reduce the number of growth inhibitors available to the tadpoles from the external pond, but may actually have served to concentrate protothecans produced within them. It is possible that *P. richardsi* accumulation was induced by raising tadpoles in closed cages, with no natural flow-through of water or nutrients. The majority of experiments on the role of micro-organisms in interference competition between anurans have employed glass or plastic containers (e.g. Richards, 1958; Beebee, 1991; Biesterfeldt *et al.*, 1993). However, Griffiths *et al.* (1993) found high numbers of protothecans in tadpoles raised in open mesh cages and Wong *et al.* (1994) found high levels of *Prototheca* in tadpoles from two natural ponds. It seems likely that some aspect of microenvironment quality, as yet undetermined, influences both competition intensity and *Prototheca* accumulation although it remains uncertain as to whether or how these phenomena are causally related under natural conditions.

Biesterfeldt *et al.* (1993) attempted to induce *Prototheca* accumulation in closed cages of tadpole-crowded pond water in the laboratory and in the field. Cages left for five days in the field consistently failed to produce inhibitors, whilst cages kept in the laboratory accumulated inhibitors within a few days. Their results suggested that *Prototheca* accumulation is inhibited by biotic and abiotic factors not present in the laboratory, such as UV light, low pH or competition with other micro-organisms. In our study, plastic cages contained water, sediment and vegetation from the main body of the pond and were exposed to the same levels of UV light and other environmental variables as the rest of the pond. Densities of tadpoles in these cages were low in comparison to laboratory stocks. Nevertheless, *Prototheca* accumulated in the faeces of tadpoles raised in these cages to levels similar to those seen in the laboratory. This evidence confirms that *P. richardsi* can attain high titre under natural levels of UV light and in the presence of other micro-organisms present in pond sediments. Manipulation of the plastic cage microenvironment should therefore provide a useful approach for further investigations of interference competition in nature.

Conclusions

We draw two conclusions from this study. Firstly, it seems clear that neither resource nor interference competition was a significant structuring force on *B. bufo* and *R. temporaria* populations in fish-ponds where predation pressure was high. *R. temporaria* tadpole densities had fallen by over 50% by the time *B. bufo* larvae were free-swimming, and continued to decrease rapidly thereafter. Top-down predation effects in such ecosystems are thus probably more important than competition in moulding the community structure of these anuran assemblages, despite the very large initial densities of eggs laid. Nevertheless, high levels of *Prototheca* may increase vulnerability of tadpoles to predation (Lefcort & Blaustein, 1995), and as suggested by Werner & Anholt (1996), it is probably futile to study competition and predation in isolation from one another. Secondly, competition can be induced in fishponds by constraining *B. bufo* with *R. temporaria* at natural densities in plastic cages. Further study is clearly required to determine how microenvironment affects competition and *P. richardsi* titres, and whether these two phenomena are causally related in the field as they appear to be in the laboratory.

Acknowledgements

We thank landowners for access to the study ponds, Dr Louise Bardsley, Dr Susan Hitchings and Donald Baker for their assistance, and the Biotechnology and Biological Sciences Research Council for financing GCB's studentship.

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Accepted: 4.3.97