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Effects of predator-induced thinning and activity changes on life history in a damselfly

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Abstract We investigated how the lethal and non-lethal presence and absence of a fish predator, perch (*Perca fluviatils*), influenced behaviour, numbers emerging, size at emergence, and development rate of the damselfly *Lestes sponsa*. The experiment was carried out in outdoor artificial ponds and spanned from the egg stage to emergence of the damselflies. During the experiment food resources for the damselflies were continuously monitored. Damselflies exposed to a lethal predator showed a significantly lower activity level than those in the absence of predators or subjected to a non-lethal predator. Half-way through the larval stage the reduction in activity level was correlated with the presence of lethal predators, and at the end of the larval stage with higher zooplankton densities. Though larvae decreased activity level, size at emergence was larger and development time faster for individuals in the lethal predator treatment. Since fewer larvae emerged from that treatment we interpret the larger size at emergence to be an effect of a combination of thinning and higher zooplankton densities.

Keywords Predator-prey interactions · Thinning · Non-lethal effects · Predator avoidance · *Lestes*

Introduction

Size and age at maturation are important life history characters in the determination of fitness (Roff 1992; Stearns 1992). In the last decade much research has focused on how non-lethal predator-avoidance behaviour and lethal effects, i.e. mortality caused by predation, affect these traits, but we have little information on the relative importance of these two effects (Werner 1992; Abrams and Rowe 1996; Reznick et al. 2001).

A wide variety of animals respond to the presence of predators by reducing foraging activity and/or increasing refuge use (Lima and Dill 1990; Lima 1998). We refer to these behavioural patterns as non-lethal effects. These effects typically result in lowered food-intake rate, which in turn reduces growth rate and development rate. Thus behavioural changes can affect important life history characters such as size at, and time to, maturity (Crowl and Covich 1990; Skelly and Werner 1990; Peckarsky et al. 1993; Ball and Baker 1996). For example, a decrease in foraging effort usually results in a long juvenile period, a late maturity and a small size at maturity. Maturing late might influence fitness, because late maturation may result in a situation where most conspecifics already have mated or the best territories may be occupied (Fincke 1982; Banks and Thompson 1987). Size at maturity might also influence fitness, because reproductive success can in many cases be directly related to the size at emergence (Banks and Thompson 1987; Moore 1990); but also see Fincke (1982) and Anholt (1991).

Predation on consumers can also influence life histories and two types of effects can be distinguished. First, a direct effect whereby predators induce a shift in life history characters of their prey by targeting those with particular traits, e.g. small or large prey (Abrams and Rowe 1996; Reznick et al. 2001). Second, an indirect effect that is mediated through the food resources of the consumer. If consumers compete for food, those that evade predation may be expected to emerge larger, and perhaps even earlier, due to a higher per capita food density. Predators removing consumer individuals may thus increase the per capita food resources, a phenomenon commonly known as thinning (Abrams et al. 1996; Van Buskirk and Yurewicz 1998). Thinning can be categorized as an indirect effect because thinning indirectly increases the resource density since resources are released from consumption. Thinning may lead to a larger consumer size, and thus affect consumer size in an opposite manner compared with the negative effect of a predator-induced

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behavioural change on size. As a consequence of these opposing forces the explanation for why consumers attain a certain size could be more complex than suggested in earlier papers (Abrams et al. 1996; Peacor and Werner 2001). However, if consumers are not food limited, no effect of thinning on size and time of emergence should be found at different food densities. If this is the case, the behavioural response of the consumers most likely determines the difference in consumers' emergence time and size in the presence and absence of predators.

Since thinning and decreased activity can work simultaneously in prey populations, and because the effects may work in opposite directions with regard to many life history traits, it is important to determine the relative importance of these effects under certain circumstances. Very few studies have separated the effects of thinning and behavioural adjustments (references in Peacor and Werner 2001), and in those doing so, resource densities have not been estimated, which is a very important trophic level in this context (Van Buskirk and Yurewicz 1998; Peacor and Werner 2001).

Damselflies are suitable for studying the simultaneous effects of behavioural avoidance and thinning. Odonate larvae are aquatic (Corbet 1962). After months to years, the larvae emerge from the water surface and moult to adults that are capable of flying. After emerging and moulting the adults must feed for a brief period before reproducing. The post-emergence/pre-maturation interval is generally much shorter than the period of larval development. In this study we examine how behaviour, survival to emergence, size at emergence, and development rate of the damselfly, *Lestes sponsa*, is affected by predator presence and food availability. We studied this by manipulating predation risk and food resources in outdoor artificial ponds. As a predator we used perch (*Perca fluviatilis*) and as prey we used zooplankton. We asked the following questions:

1. Do *Lestes sponsa* larvae reduce their levels of activity in the presence of the predators and, if so, how does this affect life history characters?
2. Does thinning occur and, if so, how does this affect life history characters?
3 Does activity, food resources or thinning have the strongest effect on life history characters?

Materials and methods

All experiments were run at Umeå University, Sweden. Our target species was the damselfly *Lestes sponsa* (Odonata: Zygoptera), hereafter called *Lestes*. This species has a 1-year life cycle and overwinters in the egg stage. Though more common in lakes without fish, it can also be found sympatric with fish across Europe (Macan 1966; F. Johansson unpublished data). The larvae used in our experiment were collected as eggs following the method of Johansson et al. (2001) from a fishless freshwater pond at the University of Antwerp, Belgium, in February 2000. We used perch as the predator species. Perch is one of the most common fish predators in Sweden (Svärdson 1976) and feeds on odonates (Rask 1986). Perch were collected from Lake Brunnsjön, 16 km from Umeå. When not used in the experiment, the perch were kept in 600-l holding tanks and fed a mixture of frozen chironomid larvae and living zooplankton. As prey for perch and *Lestes* we used zooplankton collected from a fishless pond 10 km from Umeå.

Experimental set-up

The *Lestes* eggs collected were taken to a laboratory at Umeå University and kept in a controlled moist environment at 5°C until March 2000. Eggs were initiated to hatch on 15 March by submerging them in water-filled plastic tanks in a 12:12 h light regime cycle and a temperature of 20°C. Larvae hatched after 3–4 days. After hatching the larvae were divided into eight groups, each kept in small tubs (diameter 30 cm, height 12 cm) filled with 5 l water. Every day, for the first 5 weeks, the small damselfly larvae were fed with brine shrimp larvae (*Artemia*). To simulate predator presence a perch was submerged in six of the tubs for 2 min twice every week. The larvae in these six tubs were later used in the fish-presence treatments (see below).

The experiment was run in large, opaque plastic tanks (diameter 54 cm, height 34 cm). The tanks were set up indoors on 1 April, and filled with 55 l tap water. Light was provided by fluorescent tubes and the temperature was 20°C. Dry grass collected outdoors was added to each water-filled tank to induce production of rotifers in the system. Two weeks after the addition of grass ten *Daphnia magna* were added to each tank to initiate zooplankton cultures. The zooplankton were then left in the tanks to multiply, for 2 weeks before *Lestes* were introduced. Aeration of the water was provided by an airpump system. Perch were submerged twice a week in the large containers that later (8 May) would be used for the predator-presence treatments. On 26 April the tanks were moved outdoors and we introduced 33 *Lestes* larvae into each tank, giving a density of 165 larvae/m^2. This density is within the range of natural densities found (Duffy 1994). Larvae were in instar F6–F5 (where F0 denotes last instar, F1 second last instar and so on) when introduced into the plastic tanks. In addition to the prey already present in the tanks, *Lestes* larvae were also fed brine shrimp larvae during the first week in the tanks. To prevent zooplankton density crashes and to keep the damselfly larvae from depleting food-source zooplankton, we added equal amounts of zooplankton to each tank once every week for the remainder of the experiment.

On 8 May the following treatments were added to the tanks:

1. Fish predation on *Lestes* and zooplankton (FP). This was done by enclosing a perch in a plastic cage within the tank. The cage (diameter 18 cm, height 50 cm) was placed vertically in the centre of the tank. The mesh size of the cage was 6 mm, which allowed both zooplankton prey and damselflies to enter the cage.
2. Fish present but no predation (FS). The fish was held in the same kind of enclosure as in FP except that the mesh size was 0.15 mm. This mesh size allowed fish cues to be present in the water but prevented predation on zooplankton and *Lestes* larvae.
3. No fish (N). In these tanks an enclosure similar to that in FP was placed in the tank but no fish were enclosed.

Each treatment was replicated 6 times giving a total of 18 tanks. Tanks were positioned in blocks of three in a 6×3 pattern. Fish tanks (FP and FS) had fish present only 3 days a week (Monday–Wednesday) to prevent the effective predator from depleting the tubs of *Lestes*.

Zooplankton densities were monitored in all tanks on four occasions (25 May, 8 June, 30 June, 17 July) during the experiment. Densities were estimated by filtrating 4.5 l water from every tank through a net with a mesh size of 0.5 mm. The zooplankton was thereafter preserved in 70% alcohol until counted in the laboratory with the aid of a microscope. We calculated a mean zooplankton density across all four sample days.

When the first larvae started to emerge, all tanks were checked for emerging damselflies 3 times a day (0800, 1200, 1800 hours) during the entire period of emergence (28 June–20 August). The date at which every damselfly emerged was noted and used to estimate the mean hatching date in the different treatments, and the means were later used as an estimated development rate. All exuviae and adults associated with their respective exuviae were collected. Adults were dried at 60°C for 72 h immediately after hatching, and dried adults were weighed to obtain an estimate of adult weight. The size of emerging individuals was estimated by measuring the right hind tibia of every exuviae. We used the size of exuviae rather than the size of adults, since this increased our sample size, as some adults left the tanks before we could capture them. This study (see below) and previous studies have shown a correlation between size of exuviae tibia and weight of the adult (Falck and Johansson 2000). Hence, the life history variables we analysed were size at emergence (mm) and development rate (days).

Behavioural observations

We recorded the behavioural pattern of the damselfly larvae twice, to determine if there was any treatment effect on the behaviour of the damselflies. The first survey was conducted on 1 June, when the larvae were in F3 and F4, and the second on 29 June when larvae were in F0 and F1 instar. During both surveys each tank was observed for 15 min. At the beginning of every observation period we noted the number of exposed damselfly larvae. We performed the behavioural observation on at least two and at most four of these larvae per tank. Two basic types of behaviour were recorded. Swimming, defined as a larva leaving the substrate and moving through the water column by swinging its abdomen and lamellae, and walking, defined as a change in position on the substrate when a larva moved its legs. The following types of swimming and walking behaviour were used for analysis of behaviour: (1) number of swimming events per individual, (2) total distance swum per individual, (3) mean swimming distance per swimming event, (4) number of walking events per individual, (5) total walking distance per individual, and (6) mean walking distance per walking event. The data used in the statistical analysis were entered as mean behaviour per tank.

We did not measure the spatial distribution of the larvae in the different tanks. Larvae did, however, react behaviourally to the presence of predators and predators preyed on the *Lestes* larvae in the FP treatment. The predation on the *Lestes* larvae, showed that larvae were using both the inside and outside of the enclosures in the FP treatment.

Statistical analysis

The life history variables, mean size at emergence and development rate of *Lestes*, were analysed with ANCOVA using zooplankton density as a covariate and treatment as a factor. We used mean zooplankton densities from all our four sampling dates as the covariate. Predation treatment effects on the number of emerging *Lestes* and the density of zooplankton were analysed using ANOVA. Because the behavioural variables might be interdependent we analysed these with principal component analysis (PCA). We used the correlation structure among the variables without rotation, as rotation did not increase the interpretation of the results. Separate PCAs were performed for each of the two days (1 June and 29 June) on which we performed the behavioural observations. The scores from PC1 were used in ANCOVAs with predator treatment as a factor and zooplankton density as a covariate. In this ANCOVA we used the estimates of zooplankton densities corresponding to the date the behavioural observations were made, i.e. not the mean of zooplankton densities. All data were ln(x)-transformed if necessary to meet assumptions of normality. All interaction terms in the ANCOVAs were removed from the analysis since they were always non-significant.

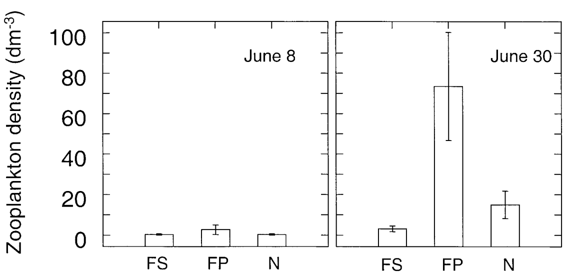

Fig. 1 Mean zooplankton density (±1 SE) in the predation treatments on 8 June and 30 June. *FS* presence of a non-lethal fish predator, *FP* presence of a lethal fish predator, *N* no fish present

Results

Zooplankton

Since the density of zooplankton might influence behaviour, we estimated zooplankton density on two dates close to the dates when we observed behaviour. Mean zooplankton densities did not differ among treatments on 8 June (Fig. 1; ANOVA, P=0.43, $F_{2,15}$=0.87). In contrast zooplankton differed among treatments in the latter part of the study, on 30 June (Fig. 1; ANOVA P<0.001, $F_{2,15}$=11.23), and Tukey's test showed a significantly higher mean density of zooplankton in treatment FP than in treatment N and FS (P<0.05 and P<0.001, respectively). No significant difference between N and FS was found (P>0.05; Tukey's test).

Behaviour

PCAs on the behavioural variables from the 2 observation days showed that PC1 and PC2 together explained 91% and 95% of the variation for the 2 days, respectively. Because PC1 explained most of the variation, and was highly correlated with all variables (Table 1), we

Table 1 Loadings from the principal components analysis (*PCA*) of the six behavioural variables and the % of the variance explained. Observations of behaviour were performed on 1 June and 29 June

	PC1	PC2
1 June		
Swimming events	0.76	0.54
Total swimming	0.83	0.53
Mean swimming	0.81	0.41
Walking events	0.75	–0.57
Total walking	0.81	–0.56
Mean walking	0.87	–0.36
% Of total variance explained	65.5	25.7
29 June		
Swimming events	0.84	0.48
Total swimming	0.86	0.50
Mean swimming	0.91	0.27
Walking events	0.87	–0.46
Total walking	0.90	–0.42
Mean walking	0.90	–0.34
% Of total variance explained	77.4	17.5

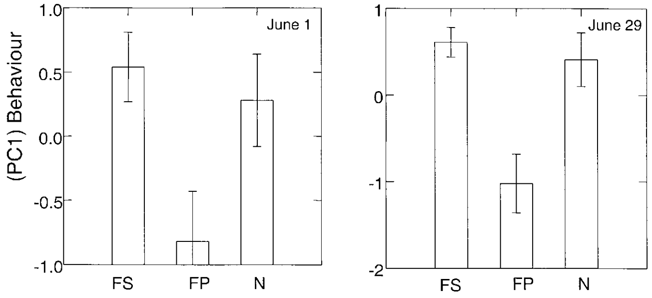

Fig. 2 Mean scores of foraging behaviour of *Lestes sponsa* larvae (±1 SE) in the predation treatments for 2 days; 1 June and 29 June. Abbreviations as in Fig. 1

Table 2 Summary of ANCOVAs on behaviour and the life history characters mean size at emergence and development rate, with predator treatment as a factor and zooplankton [ln(x+1) transformed] as a covariate

Source of variation	*df*	*F*	*P*
Behaviour 1 June			
Treatment	2	2.92	0.08
Zooplankton	1	0.96	0.34
Error	14		
Behaviour 29 June			
Treatment	2	2.20	0.14
Zooplankton	1	3.91	0.07
Error	14		
Mean size			
Treatment	2	3.48	0.06
Zooplankton	1	0.04	0.83
Error	14		
Development rate			
Treatment	2	2.42	0.12
Zooplankton	1	10.58	0.005
Error	14		

used the scores from PC1 to analyse zooplankton and predation effects on behaviour. Larvae displayed the types of behaviour recorded less frequently in the presence of lethal predators (Fig. 2), but results from the ANCOVAs suggest that this was not caused by predator presence only. For 1 June, the ANCOVA of the scores indicated a treatment effect, suggesting that larvae were less active in the presence of a lethal predator; FP treatment (Table 2, Fig. 2). In contrast, on 29 June we found a zooplankton density effect. This suggests that zooplankton caused a decrease in the types of behaviour displayed in the FP tubs later on in the season, when larvae had developed further and were close to emergence (Table 2, Fig. 2). In summary, larvae showed less behavioural activity in the presence of a lethal predator but late in the season this reduction in activity was caused mainly by higher zooplankton densities.

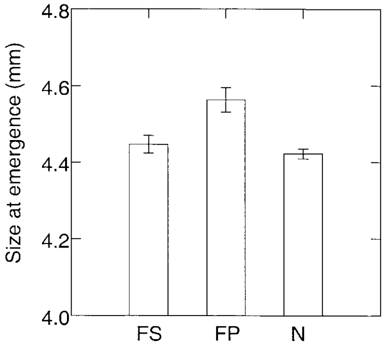

Fig. 3 Mean size at emergence of *L. sponsa* larvae (±1 SE) in the predation treatments. Abbreviations as in Fig. 1

Numbers emerging

As expected, fewer adults emerged from the FP treatment (mean=4.33±0.49 SE) than from the other two treatments (mean=11.5±1.52 SE and 11.67±0.61 SE; N and FS, respectively). The result was supported by ANOVA (P<0.001, $F_{2,15}$=28.82) and Tukey's test showed that numbers emerging was significantly lower in FP compared to the other two treatments (P<0.001). This difference is taken as evidence for a higher mortality rate in the FP treatment compared to the other two treatments, and thus one important prerequisite for a thinning effect is fulfilled, namely a difference in consumer density caused by predation. There was no difference in number of emerging adults between FS and N (Tukey's test, P>0.95).

Size at emergence

There was a correlation between the dry weight of the adult and the length of the right hind tibia of its exuviae (r^2=0.31, P<0.001, n=102). Therefore using tibia length as an overall size estimate seems valid. Zooplankton densities did not affect size at emergence, although treatment had a marginally significant effect (Table 2). Therefore we removed zooplankton density from the analysis and performed a one-way ANOVA on the effect of treatment. This ANOVA showed an effect of treatment, suggesting that larvae from the FP emerged at a larger size than larvae from other treatments (P<0.001, $F_{2,15}$=10.02; Fig. 3). Tukey's test performed subsequently supported this interpretation, as larvae from both N and FS were smaller than larvae reared in FP (P<0.01 and P<0.01 respectively). There was no difference in size at emergence between N and FS.

To explore the suggested outcome of the ANCOVA, that zooplankton densities does not affect size at emergence of *Lestes*, we regressed mean size of *Lestes* on zooplankton density. This regression showed a strong correlation between the two variables indicating that zooplankton densities do in fact affect size of *Lestes* (r^2=0.40, P<0.005, n=18). Hence, there is a colliniarity between zooplankton and treatment and therefore it is

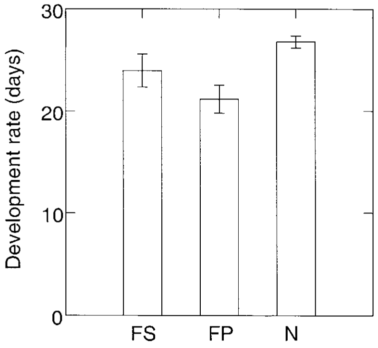

Fig. 4 Mean development rate of *L. sponsa* larvae (±1 SE) in the predation treatments. Abbreviations as in Fig. 1

impossible to specify whether treatment or zooplankton caused the increase in size in the FP treatment.

Development rate

Development rates of the damselfly larvae were affected by zooplankton densities but not by treatment (Table 2). A subsequent one-way ANOVA where zooplankton was removed from the analysis suggested that larvae from the FP treatment had a faster development rate than larvae in the N treatment ($P<0.05$, Fig. 4). This difference is, however, mainly an effect of zooplankton densities, supported by the fact that zooplankton densities were positively related to development rates of *Lestes* in a regression analysis ($r^2=0.34$, $P<0.05$, $n=18$).

Discussion

The experiment showed that the predators affected the consumers in two different ways. The presence of perch in the FP treatment reduced foraging activity and decreased population density of the *Lestes* larvae. Although the activity depression was strong, no decrease in size at emergence was found in the *Lestes* larvae. Instead, larvae emerged at a larger size and developed faster in the presence of the lethal predators, suggesting that in this experiment, the effect of thinning and/or zooplankton density was more important for life history traits than the reduction in behaviour.

The presence of lethal predators considerably reduced the activity of the *Lestes* larvae. A decrease in foraging effort of *Lestes* larvae in the presence of perch has also been found in a laboratory experiment (Stoks and Johansson 2000). Even if we did not measure foraging behaviour explicitly, the types of behaviour estimated could be considered to be important determinants of foraging rate. Swimming and walking are associated with changes in foraging site, and damselflies move more often when food patches are depleted, and thereby gain access to new and better foraging patches (Heads 1986). A decrease in the types of behaviour like those used in our study has been shown to decrease growth in several aquatic organisms including damselflies (Dixon and Baker 1988; Skelly and Werner 1990; Suhling 2001). Hence we should expect the larvae with reduced activity to grow less and emerge at a smaller size given that development time did not differ between treatments.

The decrease in activity levels of *Lestes* in the FP treatment did not cause a decrease in size at emergence. Instead these larvae showed an increase in size at emergence and a shorter development time. We suggest that this is an effect of thinning, since the predators increased mortality in the FP treatment. It is therefore very likely that the larger size at emergence in the predator treatment was a result of increased per capita food for the *Lestes* larvae. The higher per capita food density in our experiment could be mediated in two ways. First, by removing *Lestes* larvae, the predators could cause an increase in per capita food density as an effect of lower *Lestes* density. Second, by predation release from the *Lestes*, zooplankton densities increased to densities above those in the other two treatments causing even higher per capita effects. While past studies have ignored the effects of resources when trying to separate the effects of thinning and behavioural adjustments (e.g. Van Buskirk and Yurewicz 1998 ; Peacor and Werner 2001), our study pinpoints the need to account for resource density when trying to understand effects of behaviour and thinning.

It could be argued that the lower activity in the latter part of our study (29 June) was an effect of higher zooplankton densities, since zooplankton densities were higher in the FP treatment. According to theory the response to increasing food levels is usually hump-shaped, with an initial increase in activity at low to intermediate food densities, and then a decrease in activity at higher food densities (Ware 1975; Sih 1984; McNamara and Houston 1994). Hirvonen (1999) found support for this prediction in a short-term laboratory experiment on *Lestes sponsa* larvae. We do not know where on this curve our larvae were positioned during the experiment and therefore cannot conclude to what extent zooplankton densities influenced behaviour during the latter part of our experiment. We would, however, like to note that theory predicts that under long-term high resource densities, which were likely to have been attained in our experiment, animals should in fact reduce activity in the presence of predators (McNamara and Houston 1994). We would also like to emphasize that when zooplankton densities did not differ among treatments (1 June), larvae still showed a low level of activity in the presence of lethal predators. Additionally, when lethal predators are present a decrease in activity even at high food levels is predicted (Werner and Anholt 1993). We therefore consider it likely that the reduced activity in the earlier part of our experiment was only an effect of the presence of lethal predators, and during the latter half of our experiment (29 June) the reduction in behaviour was a combined effect of predation risk and higher zooplankton densities.

The higher density of zooplankton in the FP treatment when this was measured for the second time could have been caused by predation release from the damselflies, allowing a higher growth rate of the zooplankton population. It could also be an effect of increased nutrient recycling mediated through faeces from the fish. However, if this latter explanation was valid we would have observed the same increase in zooplankton in the FS treatment, which was not the case.

An alternative explanation for the larger size of the larvae in the FP treatment could be negative size-selective predation by fish. We think that this is very unlikely because perch in the size ranged used are usually positively size selective with regard to invertebrates (Rask 1986).

Other studies of simultaneous thinning and behavioural alterations in a simple three-link system have found a mixture of effects regarding growth and development of consumers. Studies on damselflies have found no effect of thinning but an effect related to reduction in feeding behaviour, which caused a reduced growth effect (McPeek 1990, 1998; Stoks et al. 1999). These studies differ from ours in two respects. First they used only larvae from the final two instars (hence a shorter time period) for the experiments. Second, the experiments were performed in field enclosures allowing prey to move in and out of the enclosures, which may reduce treatment effects on resource availability. Whether the difference between our result and others is caused by the duration of the experiments, experimental design or differences between systems should be addressed in future studies. Similar differences between species and experiments with regard to thinning and behavioural effects have been found in amphibians (Wilbur 1987; Semlitch 1987; Van Buskirk and Yurewicz 1998). For example Van Buskirk and Yurewicz (1998) found an increase in growth in tadpoles despite a decrease in foraging activity, suggesting that thinning was more important than the behavioural effect in their system. In contrast Semlitch (1987) found that predators restricted activity of salamanders, which resulted in a smaller size of surviving salamanders in the presence of predators.

Previous studies have shown that aquatic invertebrates including *Lestes* larvae reduce their activity even though the predator cannot cause a lethal effect (Stoks and Johansson 2000). We did not find a decrease in activity in the FS treatment. Hence, our initial attempt to create an effect of activity reduction without thinning failed, and we could therefore not obtain a quantitative estimate of activity reduction on life history characters. The mesh size used for fish enclosure in the FS treatment was fine, and possibly water circulation between the enclosures with the perch and the outer water column was lower than in the FP treatment where the mesh size was larger. We did, however, check that water circulated through on several occasions. Other studies have shown that the behavioural effects are generally stronger when predators can forage freely (Van Buskirk and Yurewicz 1998). The reason for this stronger response is believed to be an effect of chemical cues released when conspecifics are preyed upon (Chivers et al. 1996). Hence, a larger mesh size or cues from conspecifics being preyed upon might have caused a stronger activity response to the predators. Nevertheless, the lack of a difference in life history characteristics between the FS and the N treatment fits well with our finding that larval behaviour and zooplankton densities did not differ in these two treatments.

In summary, our study suggests that indirect effects on life histories, mediated by resource densities, may exceed indirect effects mediated by behavioural adjustments that are commonly reported in the recent literature (Skelly and Werner 1990; Peckarsky et al. 1993; Ball and Baker 1996). Size at emergence of *L. sponsa* larvae increased even though activity was reduced. Since size at emergence is positively related to fecundity in many animals (Roff 1992), the effect of increased predation is not necessarily negative when focusing on the level of population dynamics. In fact, an increase in predation could cause higher densities in the next generation if density reduction of the prey is not too low (Wilbur 1988).

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