Effects of *Anisops sardea* (Hemiptera: Notonectidae) on oviposition habitat selection by mosquitoes and other dipterans and on community structure in artificial pools

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Abstract

We investigated the effects of the predatory backswimmer, *Anisops sardea*, on oviposition habitat selection of mosquitoes and other dipterans, and on community structure in experimental pools. We predicted that those dipteran species whose larvae were shown to be highly vulnerable to predation by *Anisops* would avoid *Anisops* pools when choosing an oviposition site. We established the following treatments in plastic tubs: (1) Control (without *Anisops*); (2) Free *Anisops* (ten *Anisops* within pool but not caged); (3) Caged *Anisops* (ten *Anisops* in cage). The pools were open to colonization by insects. We added resting stages of crustaceans and first instar larvae of the mosquitoes *Culiseta longiareolata* and *Culex laticinctus*. Among the dipteran species, *Culiseta longiareolata*, *Culex laticinctus*, *Chironomus riparius* (Chironomidae) and *Forcipomyia* sp. (Ceratopogonidae), only *Culiseta* larvae were highly vulnerable to predation. As predicted, based on larval vulnerability, *Culiseta*, but not the other species, avoided *Anisops* pools when ovipositing. Free *Anisops* reduced taxon richness. This reduction resulted largely from the elimination of the cladoceran *Ceriodaphnia* sp. and *Culiseta* in most free *Anisops* pools. Thus, *Anisops sardea* structures the community, both by a behavioral response of prey to its presence and by consumption of prey.

Introduction

Predators can have profound effects on populations and community structure in aquatic systems (Sih et al., 1985; Wilbur, 1997). These effects can come from direct consumption, induced responses by prey species to risk of predation, and indirect interactions resulting from both consumption and behavioral responses. Direct consumptive effects often contribute to changes in community structure based on size-selective predation (Zaret, 1980). Induced responses to risk of predation include alterations in how much, where, and when a species forages (Koperski, 1997, 1998; Moses & Sih, 1998), developmental decisions (Chivers et al., 1999; Riessen, 1999; Peckarsky et al., 2001; Spencer

& Blaustein, 2001), morphological changes (Barry, 2000) and where a female chooses to oviposit (Resetarits, 1996; Blaustein, 1999). Indirect effects include increased success of a prey species of low prey preference because of relaxed interspecific competition caused by a reduction in density or activity of a superior competitor (Hampton et al., 2000), and trophic cascades caused by a reduction in density or activity of consumers of algae in tritrophic systems (Arner et al., 1998; Bertolo et al., 2000).

Predatory backswimmers (Notonectidae) are ubiquitous and often abundant in temporary and permanent pools, and may greatly influence the aquatic community. Predatory effects of the genus *Notonecta* have received considerable attention. *Notonecta* have

been shown to affect oviposition habitat selection in some species of mosquitoes (Chesson, 1984; Blaustein et al., 1995; Blaustein, 1998; Spencer et al., 2002), influence prey abundance and community structure through differential prey preference (Murdoch et al., 1984; Arner et al., 1998; Blaustein, 1998), and cause trophic cascades (Blaustein et al., 1995; Arner et al., 1998).

Anisops spp. are smaller-bodied backswimmers (ca. 8 mm in length and 2 mm in width for *Anisops sardea* Herrich-Schaeffer vs. 14 mm in length and 4.5 mm in width for *Notonecta maculata* Fabricus), which are also found in high densities in late-season temporary pools (e.g., Lahr et al., 1999), as well as in permanent pools (e.g., Barry, 1997). They have received less attention than *Notonecta* with regards to their predatory effects. Laboratory studies on several *Anisops* species suggest that they can affect communities in various ways. Both *A. sardea* (Tawfik at al., 1986) and *A. bouvieri* Kirkaldy (Nishi & Venkatesan, 1998) preyed heavily on *Culex* mosquitoes in the laboratory. *Anisops wakefieldi* White was shown to be a very efficient predator of the cladoceran *Ceriodaphnia dubia* Richard (Gilbert & Burns, 1999), and *A. danei* (Brooks) preyed efficiently on small size-classes of *Daphnia thomsoni* (Sars) (Reynold & Geddes, 1984). Several *Anisops* species were shown to induce the development of crests in *Daphnia* spp. (Grant & Bayly, 1981; Barry, 2000), which reduce their vulnerability to predation (Barry & Bayly, 1985). Barry (1997) concludes that *Anisops* predation may be the main factor regulating *Daphnia* populations during the winter in Australia.

Of interest here are the effects of *Anisops sardea* on oviposition habitat selection, population abundance of prey species and community structure in pools. Potential prey for *Anisops* in natural rock pools of northern Israel include four dominant dipteran species: the mosquitoes *Culiseta longiareolata* Macquart and *Culex laticinctus* Edwards, the midge *Chironomus riparius* Meigen and the ceratopogonid *Forcipomyia* sp. The following conditions may increase the likelihood for evolving oviposition habitat selection in response to risk of predation (see Blaustein, 1999): (1) females lay their eggs together (all eggs 'in one basket') and have few opportunities to oviposit in their lifetime; (2) females can choose among several patches in which to oviposit; (3) among-patch distributions of predators are random or contagious; (4) among-patch distribution of predators are largely fixed from the time a prey female has oviposited until her progeny can leave the

patch; (5) immature stages are prone to high mortality from predation. For all four diperans, the first four criteria are met with regards to *Anisops*, but their vulnerability to this predator is unknown. We predict that only those species whose larvae are shown to be highly vulnerable to predation by *Anisops* would avoid *Anisops* pools when choosing an oviposition site. Here, we test these predictions in an outdoor artificial pool experiment. We assess the risk of predation for each dipteran species, and examine the effects of the presence of *Anisops* on their oviposition.

Anisops may affect pool communities quite differently from *Notonecta*. For example, the much larger *N. maculata* is capable of preying on fairly large anuran tadpoles (Blaustein & Kotler, 1997), while *A. sardea* is not (Yaffe & Blaustein, unpubl. data). We have found that late instars of *N. maculata* reduce populations of the larger-bodied cladoceran *Daphnia magna* Strauss (1∼3 mm), but not of the smaller-bodied cladoceran *Ceriodaphnia* sp. (∼0.6 mm) (Eitam et al., unpubl. data). However, given that other *Anisops* species reduce densities of *Ceriodaphnia* (Gilbert & Burns, 1999) and because of the size differential between *Notonecta* and *Anisops*, we predict that *Anisops sardea* would reduce densities of a relatively small cladoceran like *Ceriodaphnia*. In this paper, we study the effects of *A. sardea* on taxon richness and on densities of *Ceriodaphnia*, and compare these effects with those of *Notonecta*.

Materials and methods

We conducted an outdoor experiment under a canopy of *Pinus halepensis* Mill. on the University of Haifa campus. On 18 May 2000, we filled 18 plastic tubs (48 × 27 cm at bottom, 55 × 33 cm at top, height 19 cm) with 20 liters of tap water. Such artificial pools are within the size range of natural pools where *Anisops* and the prey species of interest are found (Blaustein, pers. obs.). On 19 May, we added the following: 250 cm^3 of *Quercus calliprinos* Webb leaf litter; 5 ml of 20:20:20 powdered NPK fast release inorganic plant fertilizer (providing two potassium ions to two phosphate ions to one each of ammonium and nitrate); 250 ml of water from other artificial pools, filtered twice through a 250 μm mesh net. The litter and NPK provided a source of nutrients, and the filtered water provided an inoculum of algae and micro-invertebrates. After some initial evaporation, we maintained water volume at approximately

15 l by adding aged tap water. Tubs were uncovered allowing for colonization by aquatic insects. Colonization by predators was very rare but when it occurred, the predator was removed.

We suspended a cage with a cord from the top of each of the 18 tubs, and placed it in a horizontal orientation so that most of the cage was submerged. The cages were constructed of 19×8 cm clear plastic cylinders closed on both ends with mosquito screening (mesh size: 2 mm). On 30 May, we established the following treatments, each with six replicate pools: (1) Without *Anisops* (control); (2) Ten *Anisops sardea* (mixture of 4th and 5th instar nymphs and adults) within the cage ('caged *Anisops*'); (3) Ten *Anisops* within the tub and outside of the cage ('free *Anisops*'). This density is well within the range of *Anisops* densities in natural pools. The caged predator treatment allowed us to differentiate whether any reduction in the number of eggs in free-predator pools may be due to either oviposition habitat selection or to predation on either the ovipositing female or the eggs themselves. Approximately once per week, we checked *Anisops* abundance and replaced dead or missing individuals. One control tub was vandalized and overturned on 4 June, and was excluded from the study.

We removed fallen pine needles daily to allow clear observation. To estimate oviposition habitat selection of mosquitoes, we removed egg rafts daily and identified each raft to genus (*Culiseta* or *Culex*). We reared rafts of *Culex* in the laboratory for species identification of fourth instar larvae. All *Culiseta* egg rafts were *C. longiareolata*.

To estimate treatment effects on mosquito survival (i.e., vulnerability of larvae to predation by *Anisops*), we introduced 45 first instar *Culiseta longiareolata* and 30 first instar *Culex laticinctus* larvae to each tub on 22 June. We subsequently counted larvae and pupae of both species by observation on 3 July. In three pools (one caged *Anisops* and two free *Anisops* pools), poor visibility due to algae did not allow accurate counts. Consequently, these pools were not considered in the analysis of mosquito immature abundance.

We estimated oviposition habitat selection by *Forcipomyia* sp. (Diptera: Ceratopogonidae) and *Chironomus riparius* (Diptera: Chironomidae) by counting egg masses of each species, on 20 June and 25 June. Data from both dates were pooled before analysis. We estimated vulnerability of these species to predation by counting pupae of *Forcipomyia* and pupal exuviae of *Chironomus* on the same dates (as our best estimates of emergence), and then calculating the ratio

between the number of pupae or pupal exuviae and the number of egg masses for each species. These ratios are rough estimates, assuming that oviposition patterns on the two dates in which they were measured are representative of earlier dates on which the collected pupae and or pupal exuviae were deposited as eggs. For *Chironomus*, pools in which no egg masses were observed (two pools from each treatment) were not included in the analysis of this ratio.

The most abundant species in the pools was *Ceriodaphnia* sp. We estimated relative density of this species by two sweeps with a 10×7 cm net (mesh size: 250 μm) across the width of each pool, one sweep at each end, on 21 June. We estimated taxon richness by three S-shaped sweeps through each pool with a 15×11 cm net (mesh size: 250 μm), plus visual observation, on 2 July.

Data were analyzed by ANOVA, and treatments compared using the Tukey-Kramer HSD test when F-values from the ANOVA were statistically significant ($P < 0.05$). All data, except for taxon richness, were square-root transformed ($\sqrt{x + 0.5}$) prior to analysis to normalize distributions (Zar, 1996).

Results

The number of *Culiseta* egg rafts was significantly lower in free *Anisops* pools than in control pools ($F_{2,14} = 4.63$, $P = 0.03$; Fig. 1a). The difference between caged *Anisops* pools and control pools was not statistically significant (Fig. 1a). However, the number of egg rafts was nearly identical in free *Anisops* and caged *Anisops* pools (indicating that there was no predation on *Culiseta* egg rafts or adults by *Anisops*). A *t*-test comparing all pools containing *Anisops*, whether free or caged, with control pools revealed fewer egg rafts in *Anisops* pools than in non-*Anisops* pools ($t = 3.12$, $df = 15$, $P = 0.007$), indicating avoidance of *Anisops* pools by ovipositing *Culiseta* females.

Culiseta longiareolata larvae and pupae were nearly eliminated in free *Anisops* pools ($F_{2,11} = 97.82$, $P < 0.001$; Fig. 1b). The abundance of *Culiseta* larvae and pupae was also significantly lower in caged *Anisops* pools than in control pools, suggesting that some larvae entered the cages as early instars and were consumed. Indeed, larvae were occasionally observed inside cages in the free *Anisops* and control treatments.
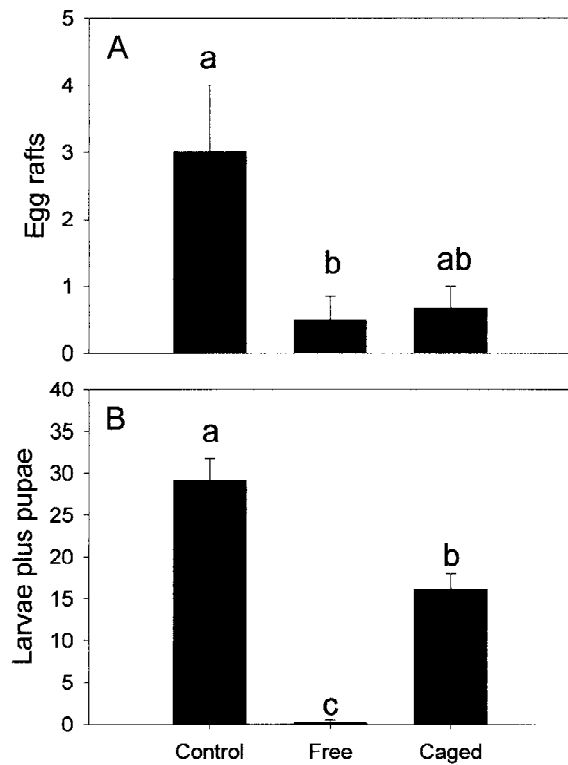
Figure 1. (A) Mean number of *Culiseta longiareolata* egg rafts laid per pool. (B) Mean number of *C. longiareolata* larvae and pupae surviving 11 days after 45 first-instar larvae were introduced to each pool. Control = no *Anisops*; Free = unconstrained *Anisops*; Caged = caged *Anisops*. Error bars represent +1 SE. Treatments with the same letter are not significantly different ($P = 0.05$) according to the Tukey–Kramer HSD test.

Figure 2. (A) Mean number of *Culex laticinctus* egg rafts laid per pool. (B) Mean number of *C. laticinctus* larvae and pupae surviving 11 days after 30 first-instar larvae were introduced to each pool. Control = no *Anisops*; Free = unconstrained *Anisops*; Caged = caged *Anisops*. Error bars represent +1 SE. Treatments with the same letter are not significantly different ($P = 0.05$) according to the Tukey–Kramer HSD test.

All *Culex* egg rafts were identified as *C. laticinctus*. The number of *Culex* egg rafts was not significantly different among treatments ($F_{2,14} = 0.44$, $P = 0.66$; Fig. 2a). The number of surviving *Culex* larvae and pupae tended to be lowest in free *Anisops* pools and highest in control pools, but differences were not statistically significant ($F_{2,10} = 1.45$, $P = 0.28$; Fig. 2b).

The number of *Forcipomyia* egg masses was not significantly different among treatments ($F_{2,14} = 0.09$, $P = 0.91$; Fig. 3a). The number of *Forcipomyia* pupae was significantly higher in caged *Anisops* pools than in control pools, with no differences between free *Anisops* and other treatments ($F_{2,14} = 5.21$, $P = 0.02$; Fig. 3b). The ANOVA of the ratio between pupae and egg masses bordered on being, but was not, statistically significant ($F_{2,14} = 3.55$; $P = 0.056$).

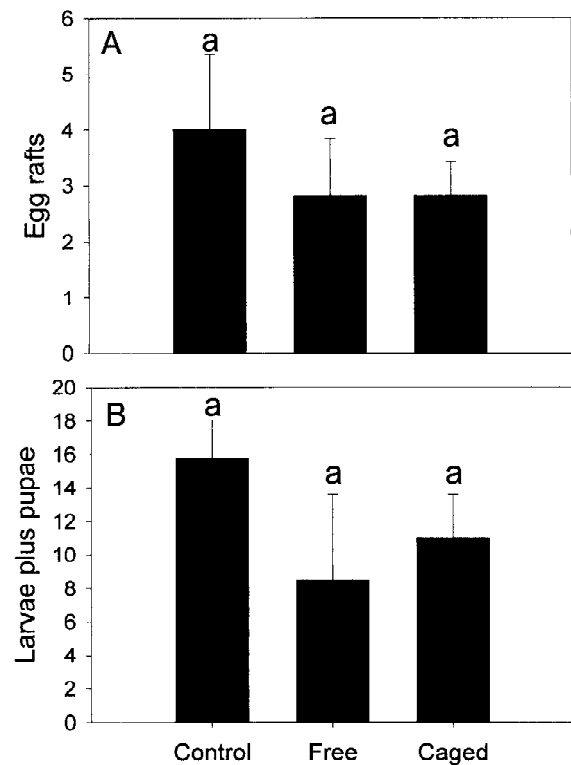The number of *Chironomus* egg masses was not significantly different among treatments ($F_{2,14} = 0.02$, $P = 0.97$; Fig. 4a). Furthermore, there were no significant differences among treatments in the number of *Chironomus* pupal exuviae ($F_{2,14} = 0.80$, $P = 0.46$; Fig. 4b), or in the ratio between pupal exuviae and egg masses ($F_{2,8} = 0.74$, $P = 0.51$).

Ceriodaphnia sp. was almost totally eliminated from free *Anisops* pools, with only one individual recovered from a single pool ($F_{2,14} = 29.91$, $P < 0.0001$; Fig. 5). The abundance of *Ceriodaphnia* was also significantly lower in caged *Anisops* pools than in control pools.

In addition to the common species reported above, other less common taxa observed in the pools included the insects ephydrid and mayfly larvae, and the crustaceans cyclopoid copepods, calanoid copepods, ostracods and *Cyzicus*. Taxon richness was considerably lower in free *Anisops* pools than in either caged *Anisops* or control pools ($F_{2,14} = 15.06$, $P = 0.0003$; Fig. 6).
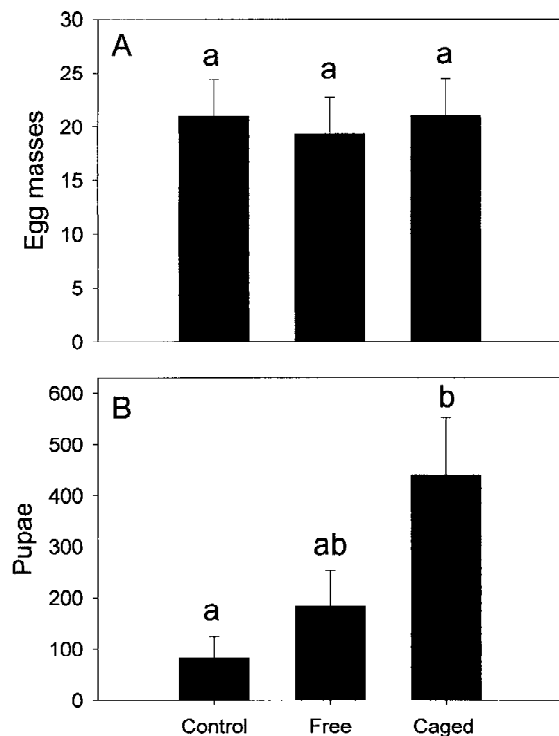
Figure 3. (A) Mean number of Forcipomyia sp. egg masses counted per pool. (B) Mean number of Forcipomyia sp. pupae counted per pool. Control = no Anisops; Free = unconstrained Anisops; Caged = caged Anisops. Error bars represent +1 SE. Treatments with the same letter are not significantly different (P = 0.05) according to the Tukey–Kramer HSD test.

Figure 4. (A) Mean number of Chironomus riparius egg masses counted per pool. (B) Mean number of C. riparius pupal exuviae counted per pool. Control = no Anisops; Free = unconstrained Anisops; Caged = caged Anisops. Error bars represent +1 SE. Treatments with the same letter are not significantly different (P = 0.05) according to the Tukey–Kramer HSD test.

Discussion

Among the four dipteran species tested, *Culiseta longiareolata* was the only species to demonstrate high vulnerability to predation by the backswimmer. The estimates of vulnerability were direct estimates for the two mosquito species but indirect and rougher estimates for *Forcipomyia* and *Chironomus*. However, even with a wide confidence interval around these indirect vulnerability estimates, they do not approach the vulnerability of *Culiseta* larvae to this predator. The high vulnerability of *Culiseta* immatures to *Anisops* is consistent with its vulnerability to a wide range of predators, including *Notonecta maculata* Fabricus, *Anax imperator* Leach nymphs, *Orthetrum* sp. nymphs, *Acanthocyclops viridis* (Jurine) and *Salamandra salamandra* L. larvae (reviewed in Blaustein, 1999), and to intraguild predation by *Bufo viridis* Laurenti tadpoles (Blaustein & Margalit, 1996). The high vulnerability of *Culiseta* larvae appears to be due to their large size (Blaustein & Margalit, 1994), their longer development time (Blaustein & Margalit,
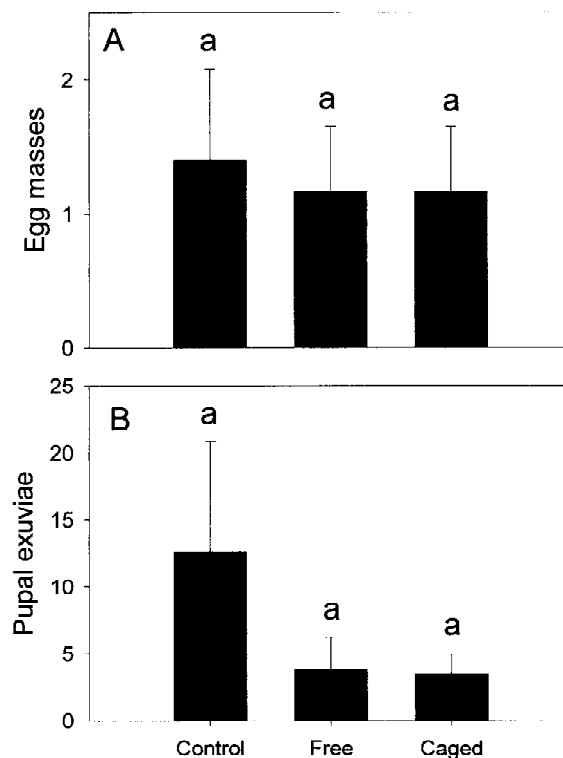
1996), their high level of activity which attracts predators, and little if any behavioral response to predators (Blaustein, unpubl. data).
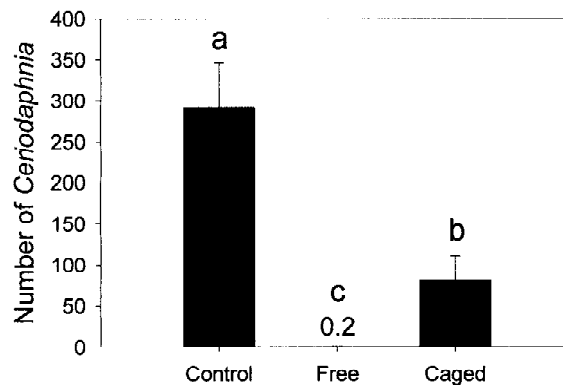

Figure 5. Mean number of Ceriodaphnia sp. sampled per pool. Control = no Anisops; Free = unconstrained Anisops; Caged = caged Anisops. Error bars represent +1 SE. Treatments with the same letter are not significantly different (P = 0.05) according to the Tukey–Kramer HSD test.

Figure 6. Mean number of taxa observed per pool. Control = no *Anisops*; Free = unconstrained *Anisops*; Caged = caged *Anisops*. Error bars represent +1 SE. Treatments with the same letter are not significantly different ($P = 0.05$) according to the Tukey–Kramer HSD test.
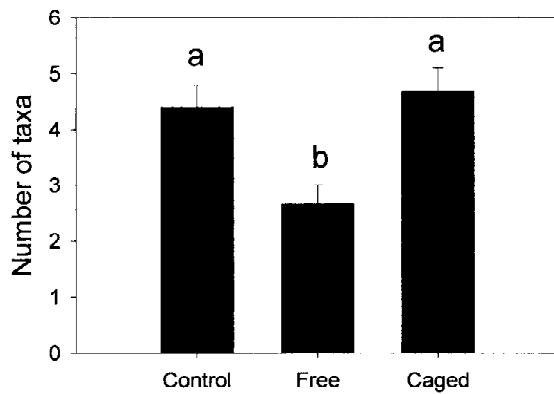
We predicted that only a species highly vulnerable to predation by *Anisops* would avoid oviposition in pools containing the predator. Indeed, only *Culiseta* showed significant avoidance of oviposition in *Anisops* pools. We have demonstrated previously that *Culiseta* avoids ovipositing in pools containing *Notonecta maculata* (Blaustein et al., 1995; Blaustein, 1998; Spencer et al., 2001) and *Anax imperator* (Stav et al., 1999). We have further found that avoidance of pools containing *Notonecta* is in response to a chemical cue (Blaustein et al., unpubl. data).

There are both similarities and differences in the effects of *Anisops sardea* and *Notonecta maculata* on community structure. Both notonectid species have negative effects on *Culiseta* and do not affect densities of *Chironomus* (Blaustein 1998; this study). However, they differ in their effects on cladocerans. *Anisops sardea* virtually eliminates the small-bodied *Ceriodaphnia*. While we did not test the effect of *A. sardea* on larger cladocerans, previous studies have shown that other *Anisops* species prefer relatively small prey. For example, Reynold & Geddes (1984) found that *A. deanei* prefers *Daphnia thomsoni* less than 2 mm in length over larger stages. On the other hand, *Notonecta* has no apparent effect on *Ceriodaphnia*, while significantly reducing densities of *Daphnia magna* (Blaustein, 1998; Eitam et al., unpubl. data). Similarly, Cooper (1983) found that *Notonecta undulata* Say prefers the largest available cladoceran prey (2.0–3.0 mm), whereas the smaller notonectid *Buenoa confusa* (which is similar in size to *Anisops*), prefers smaller prey (0.8–2.0 mm).

We have previously found that *Culiseta* reduces densities of ceratopogonids (Blaustein and Margalit,

1996; Eitam et al., unpublished data). Therefore, we would expect greater densities of *Forcipomyia* in pools in which *Culiseta* densities are reduced by *Anisops*, i.e., highest densities being in free *Anisops* pools, intermediate densities in caged *Anisops* pools, and lowest densities in control pools. The fact that the highest *Forcipomyia* densites were actually in caged *Anisops* pools is puzzling, and we can offer no likely explanation for it.

While we expected *Anisops* to decrease *Ceriodaphnia* abundance, we found the extent of the reduction surprising: virtual elimination in free *Anisops* pools and more than a two thirds reduction in caged *Anisops* pools. Though these reductions may be explained entirely by consumption, other possibilities exist. Blaustein (1997) found that caged larval *Salamandra salamandra* (where the mesh of the cage should largely exclude *Ceriodaphnia*) caused a large and significant reduction in *Ceriodaphnia* densities. He suggested that resting eggs of *Ceriodaphnia* may detect predators and hatch at a lower rate. The predation risk-hatching hypothesis has not yet been rigorously tested for this *Ceriodaphnia* species, but was demonstrated for another crustacean species when larval *Salamandra* was the predator (Spencer & Blaustein, 2001). Alternately, like *Daphnia magna* in response to predatory fish (Slusarczyk, 1995, 2001), they may produce resting eggs in response to risk of predation.

Predators, depending on their density and particular prey preference, may cause an increase, decrease or no change in species richness (Sih et al., 1985). *Anisops*, at moderate densities, caused a reduction in taxon richness in this experiment. This occurred largely due to their general elimination of two species: *Culiseta* and *Ceriodaphnia*. Decrease in species richness may be the common effect in temporary aquatic habitats. We have found similar reductions in taxon richness by moderate densities of *Notonecta maculata* (Blaustein, 1998) and *Salamandra salamandra* (Blaustein et al., 1996).

Acknowledgments

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