Influence of nymphal *Anax imperator* (Odonata: Aeshnidae) on oviposition by the mosquito *Culiseta longiareolata* (Diptera: Culicidae) and community structure in temporary pools

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ABSTRACT: We assessed the overall (consumptive plus non-consumptive) and non-consumptive effects of nymphal *Anax imperator* (Aeshnidae: Odonata) on experimental pool communities by comparing three treatments: (1) control (no *Anax*); (2) free *Anax* (*Anax* was not constrained); and (3) caged *Anax* (*Anax,* enclosed within a cage, could not consume prey outside the cages, but could possibly influence them via perceived risk of predation). Fewer egg rafts of the mosquito *Culiseta longiareolata* were found in the free *Anax* treatment compared to the other two treatments. There was no statistically significant difference in the number of egg rafts between control and caged *Anax* pools. Thus, while *Culiseta* females apparently oviposit fewer egg rafts in the presence of unconstrained *Anax*, they did not respond to predation risk from the caged *Anax*. Larval *Culiseta* densities were drastically reduced by free *Anax*; there was nearly a 100% reduction in the number reaching metamorphosis (pupae) and a 100% reduction in emergence (pupal exuviae). There were no significant treatment effects on densities of crustaceans, *Daphnia magna* and *Heterocypris* sp., or on chironomid pupal exuviae. Ceratopogonid pupal abundance was higher in free *Anax* pools than in the other two treatments toward the end of the experiment. Free *Anax* caused a trophic cascade, presumably by strongly reducing the dominant periphyton grazer, *Culiseta* larvae; periphyton mass was greater in the free *Anax* treatment than in the control. However, there was no behavioral trophic cascade, i.e., no difference in periphyton abundance between the control and caged *Anax* treatment.*Journal of Vector Ecology* **25(2): 190-202. 2000.**

Keyword Index: *Anax imperator*, *Culiseta longiareolata,* oviposition, predation risk, temporary pools.

INTRODUCTION

Predation is recognized as an important factor in the organization of many ecological communities (Sih et al. 1985), including aquatic communities (Zaret 1980). This is especially true for predation by vertebrates, with a considerable number of studies demonstrating the importance of fishes in organizing lake communities (Zaret 1980, Huang and Sih 1991, Werner and McPeek 1994, Carpenter and Kitchell 1993) and urodeles in organizing temporary pool communities (Sprules 1972, Morin et al. 1983, Morin 1987, Stenhouse et al. 1983, Fauth and Resetarits 1991, Werner and McPeek 1994, Blaustein et al. 1996. Blaustein 1997). The impact of invertebrate predators on community structure has been investigated far less in aquatic communities, but evidence has been accumulating in recent years that invertebrate predators are important organizers of aquatic community structure. This is true in both permanent habitats (Leucke and Litt 1987, Matveev 1995) and particularly in temporary pools when vertebrate predators are absent (Lounibos et al. 1987, Blaustein and Dumont 1990, Blaustein and Margalit 1994a, Fincke et al. 1997, Blaustein 1998).

There have been many attempts to ascertain the

overall impacts of a predator, and the relative importance of the direct (consumptive) and indirect (nonconsumptive) effects (Schoener 1993, Kerfoot and Sih 1987, Huang and Sih 1991, Werner 1991, Werner and McPeek 1994, Wootton 1994, Werner and Anholt 1996, Blaustein 1997). For example, it has been shown that risk of predation can reduce activity, which presumably explains reduced size at and increased time to metamorphosis in amphibians (Skelly and Werner 1990) and mosquitoes (Hechtel and Juliano 1997). Recent evidence has also been accumulating that ovipositing females can detect the risk of predation to their progeny and choose oviposition sites where such risk is lower (Chesson 1984, Rehfeldt 1990, Petranka and Fakhoury 1991, Ritchie and Laidlaw-Bell 1994, Blaustein et al. 1995, Blaustein 1998, Stav et al. 1999, Blaustein 1999).

Predators may also not only indirectly affect their prey, but also the trophic level below their prey, i.e., they can cause a trophic cascade. Although the existence of trophic cascades had been assessed most often in lakes, considerable evidence now exists that it is far from rare in terrestrial systems (Spiller and Schoener 1990, Schmitz 1994, Carter and Rypstra 1995, Hartvissen et al. 1995, Schmitz et al. 1997) and in temporary pools (Batzer and Resh 1991, Holomuzki et al. 1994, Blaustein et al. 1995, Morin 1995, Blaustein et al. 1996, Arner et al. 1998). A cascade in a tritrophic system may result from predator consumption of herbivores, which reduces herbivory and/or from nutrient recycling by the predator (Vanni and Layne 1997). Another way in which a predator can cause a trophic cascade is by altering the behavior of the prey so that herbivory is reduced. The possible existence of a behavioral trophic cascade has been given far less attention. Schmitz et al. (1997) demonstrated that non-lethal spiders caused an overall decrease in feeding rate (herbivory) and thus an increase in plant biomass. A behavioral trophic cascade is also possible if animals avoid a particular habitat while foraging or do not lay eggs in this habitat in response to risk of predation.

Mosquito ecologists have increasingly taken the approach that understanding how a predator, directly and indirectly, affects community structure is also important for understanding under what set of environmental conditions a predator will be effective in reducing mosquito populations. For example, the culling of larval mosquito populations and populations of their competitors may result in more, rather than less, mosquitoes emerging and in larger sizes of mosquitoes that emerge (Chambers 1985, Lounibos 1985). This may result if the predator's negative effect on the population via consumption is outweighed by its positive effect of relaxed intra- and interspecific competition. Species sharing the same trophic level as mosquito larvae often share predators with mosquito larvae, which in turn, affects predation intensity on mosquitoes (Bence 1988, Chesson 1989). Also very important in understanding the overall effect of a predator on mosquito populations is to determine whether mosquito species choose pools for oviposition in response to risk of predation (Blaustein 1999).

Of interest in this paper are the effects of the dragonfly *Anax imperator* on the oviposition behavior and immature densities of the mosquito *Culiseta longiareolata* and on the pool community structure in general. *Culiseta longiareolata* is the most common mosquito in temporary pools in Israel (Ward and Blaustein 1994). The larvae are primarily periphyton and detritus grazers, but they can also filter-feed on phytoplankton (van Pletsen 1981) and may also prey on small invertebrates and newly hatched tadpoles (Blaustein and Margalit 1994a). Like other odonates (Corbet 1980, Johnson and Crowley 1980), *A. imperator* is a generalist predator (Kasimov 1956). It is common in permanent and temporary pools in the region (Dumont 1991). A number of studies, particularly laboratory studies, have assessed the impact of *Anax* species on particular prey species (Blois-Heulin 1990, Werner and McPeek 1994). Numerous studies have shown that anuran tadpoles can chemically detect the presence of *Anax junius* nymphs and respond by altering their behavior (Skelly and Werner 1990, Werner 1991, Werner and Anholt 1996). Fewer studies have experimentally considered the effect of odonates on populations and communities in the field, either under natural or semi-natural conditions (Fincke et al. 1997). Laboratory experiments have shown that larvae of the mosquito, *Culiseta longiareolata*, when compared to other mosquito species, are particularly prone to predation by *Anax* (Blaustein et al., unpubl. data, Stav et al. unpubl. data) as well as by other predator species (Blaustein and Margalit 1994b, Blaustein et al. 1995, Blaustein 1998).

We found in another experiment that fewer egg rafts of *Cs. longiareolata* were found in pools containing nymphal *A. imperator* (Stav et al. 1999). Three hypotheses were put forth to explain the reduction in eggs rafts: (1) *Anax* consumes the egg rafts; (2) *Anax* consumes ovipositing females before they lay egg rafts; and (3) ovipositing *Culiseta* mosquito females can detect risk of predation from nymphal *Anax* and choose oviposition sites accordingly. In our previous study, we eliminated the first hypothesis as explaining a significant amount of this reduction (Stav et al. 1999). If *Culiseta* can detect the presence of *Anax* through a cage, then the effects of a constrained *Anax* unable to prey upon egg

rafts or ovipositing females should have similar effects of an unconstrained *Anax* on oviposition site selection. Here, we experimentally assess the effects of unconstrained *Anax* (consumptive plus non-consumptive effects) and caged *Anax* (non-consumptive effects) on *Culiseta* populations including oviposition habitat selection. We also assess the effects of caged and non-caged *Anax* on other components of the community that can affect survival and growth of *Culiseta* larvae: species sharing the same trophic level as *Culiseta* larvae (herbivorous/detritivorous crustaceans and colonizing insects) and algal mass (periphyton and phytoplankton).

MATERIALS AND METHODS

Experimental Protocol

We conducted an outdoor artificial pool experiment on the roof of the three story Biology Department building, Ben Gurion University, Beer Sheva, Israel (31°15', 34°48'). Plastic white tubs, trapeziform in cross section (34 x 59 cm at the bottom, 37 x 62 cm at the water surface), served as the artificial pools. These pools were well within the size range of natural pools containing the species of interest (Ward and Blaustein 1994, Blaustein and Margalit 1995, G. Stav, pers. obs.). We used 18 such pools in the experiment, each at least 0.5 m apart from the nearest pool in an area of 6.5 x 4 meters. On 23 February 1996, we filled the pools with tap water to a depth of 20 cm (= 43 liters). Water levels were maintained primarily with distilled water and occasionally by rains. For a nutrient source, we added 5 cm³ of ground food (30% Catlee cat food, 50% Koffolk rabbit chow, 10% yeast, and 10% Wardley fish flakes) on 24 February and on 2 March. This food supplement, in addition to allochthonous materials (dust, terrestrial insects, and occasional pigeon feces) provided a nutrient source that was probably as high as many local natural pools. Because such pools would receive considerably more radiation than natural pools, which are normally at the bottom of a shaded canyon, we placed a 90% shade net over the pools at a height of 2 m. Minimum and maximum temperatures through the course of the experiment (1 March - 21 June) were 9° and 34°C, respectively.

Because the tubs were also used in a previous experiment, we washed and soaked them in bleach and after 24 hours, rinsed them thoroughly. Despite this, on 6 April, *Daphnia magna* and ostracods (*Heterocypris* sp.) were observed in the tubs presumably having arisen from resting stages from the previous experiment. Both of these crustacean species commonly occur in pools containing *Culiseta* and *Anax* (G. Stav, pers. obs.). On

17 April, we added 100 *D. magna* adult females to each pool. Pools were left uncovered to allow for insect invasion.

The experimental design included three treatments: (1) control (no *Anax*); (2) free *Anax* (two *Anax* nymphs unconstrained with access to the entire pool and able to prey upon co-inhabiting invertebrates); and (3) caged *Anax* (two *Anax* nymphs placed inside the cage so that they could not prey upon invertebrates inhabiting the pool). Each treatment was randomly assigned to six pools. Thus, a comparison of control and free *Anax* pools should reveal the overall effects of *Anax* on particular populations, i.e., the consumptive plus non-consumptive effects. A comparison of control and caged *Anax* treatments on particular populations should reveal only non-consumptive effects.

The *Anax* cages, resting on the bottom and extending above the water, were plastic cylinders (8.5 cm diameter and 26 cm in length) closed at the bottom and covered at the top with mosquito netting of mesh size 1.5 mm². A single cage was placed in all the pools regardless of treatment to control for any effects of the cage itself. Two 5 x 17 cm submerged side windows were covered with opaque cloth of mesh size 0.5 mm² (which surrounded the cage completely) presumably allowing diffusion of any predator kairomones. The dragonfly nymphs (mean head width = 8.03 mm; standard error = 0.20) were added to the appropriate pools on 1 March. Any missing or dead nymphs were replaced with a nymph of similar size (similar size to dead nymph or to average size in the experiment if found missing). The caged nymphs were fed *Daphnia* once per week.

In prior studies on this roof (Blaustein and Margalit 1994a, 1996; Stav et al. 1999), the only mosquitoes to regularly colonize the pools were *Culiseta longiareolata*. We counted mosquito egg rafts oviposited by wild *Culiseta* females every other day. Given that *Culiseta* egg rafts take longer than 48 hours to hatch and that they are easily seen, we were able to count virtually every egg raft present during the course of the experiment. We used these egg raft data to assess the potential impacts of *Anax* on oviposition site selection. We counted *Culiseta* immatures and pupal exuviae approximately once per week from 18 April to 14 June. After this date, *Anax* began emerging as adults or died attempting to emerge. We discriminated and grouped developmental stages of *Culiseta* as follows: (1) first plus second instar larvae; (2) third plus fourth instar larvae; (3) pupae; and (4) pupal exuviae. After the mosquito emerged from the pupal skin, the exuviae remained on the water surface and could easily be counted for a good estimation of relative success in a given pool.

Chironomids and ceratopogonids also colonized these pools. Their populations were checked three times (26 April, 23 May, and 21 June) by counting chironomid pupal exuviae and ceratopogonid pupae at the air-water surface.

On 30 May, we sampled crustaceans by sweeping a 10.5 x 15.5 cm net (117 micron mesh) once across the width of the pool (37 cm sweep; volume = 6.0 liters). Samples were preserved in 75% ethyl alcohol and later enumerated under a dissecting microscope.

In order to measure treatment effects on periphyton, we vertically suspended four standard glass microscope slides (26 x 76 mm) at the center of the pool at approximately mid depth on 2 March. The slides were removed on 30 May and were air dried for 48 hours at 25°C. The material was then scraped off the slides and weighed. In each pool, the four samples were pooled and averaged for statistical analysis.

To assess treatment effects on phytoplankton, we took a 175 ml water sample from the center of each pool at mid depth on 30 May. Each sample was filtered through a Whatman filter paper (Qualitative 1), dried at 80°C for two minutes, and then weighed.

Statistical Analysis

In addition to *Culiseta longiareolata*, four other faunal groups were sufficiently common to assess for treatment effects with reasonable power: two insect taxa, chironomid species and a ceratopogonid species, plus two crustacean species, *Daphnia magna* and *Heterocypris* sp. For those dependent variables measured during only one time period (crustaceans and algae), we analyzed the data as a one-way analysis of variance. For those dependent variables measured more than once (various stages of *Culiseta*, chironomid pupal exuviae

and ceratopogonid pupae), we conducted univariate repeated measures analysis of variance. In the case of *Culiseta* egg rafts, we used total number of egg rafts combined over ten day periods as the response variable, to avoid problems caused by the number for any given day for a given pool being frequently zero. Data were natural log-transformed prior to analysis when necessary to more closely satisfy assumptions of parametric tests (Krebs 1989). The Tukey-Kramer HSD multiple comparison test was used to test treatment effects for crustaceans and algae. Linear contrasts were used in repeated measures analyses when F-values were significant.

RESULTS

Approximately 50% fewer *Culiseta* egg rafts were found in the free *Anax* pools compared to the control and caged *Anax* (Table 1; Figure 1). There was no statistically significant difference in number of egg rafts between control and caged-*Anax* pools. This same pattern was seen for larvae, pupae, and pupal exuviae (Table 2, Figure 2). There was close to a 100% reduction of the later stages and a 100% reduction in emergence (pupal exuviae) in the free-*Anax* treatment.

There were no significant treatment differences for the number of chironomids emerging from pupae as measured by pupal exuviae (Table 3; Figure 3a). Abundance of ceratopogonid pupae was higher in the free *Anax* treatment at the end of the experiment as indicated by the treatment by time interaction (Table 4; Figure 3b).

Daphnia densities tended to be higher in the free *Anax* pools compared to caged *Anax* and control pools, though the difference was not statistically significant

Table 1.   Repeated measures analysis of variance of number of *Culiseta longiareolata* egg rafts per 10 day periods, that were laid in the different treatments. Data (X+1) were natural log transformed prior to analysis. Within subjects degrees of freedom derive from Geiser-Greenhouse adjustments because the assumption of sphericity was not met.

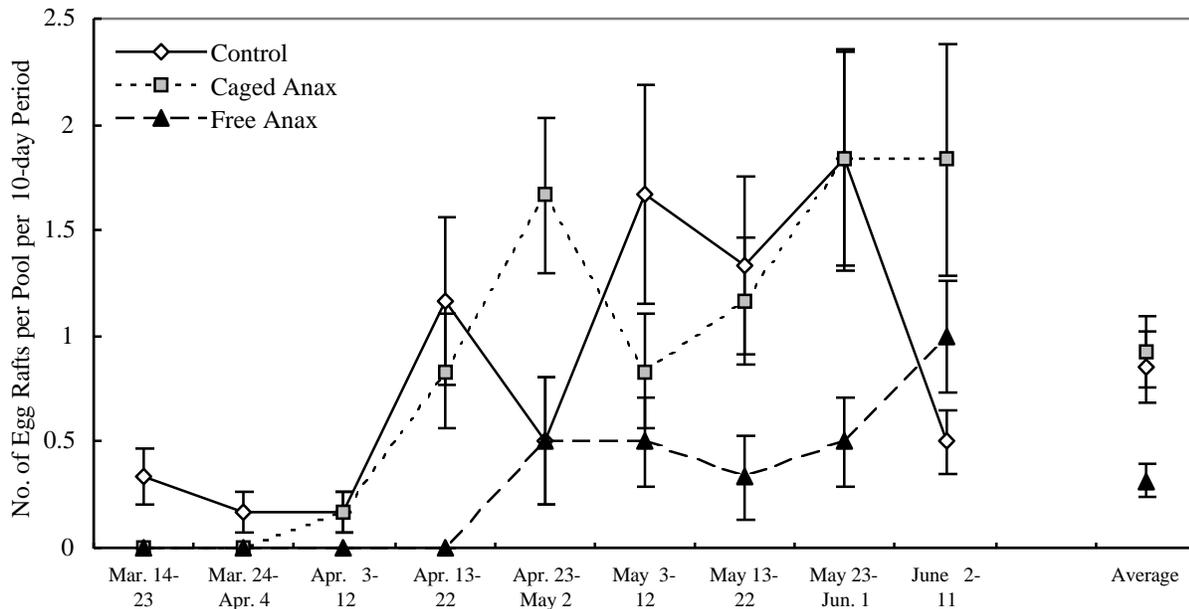| Source	df	F	P
Treatment (A)	2	3.80	0.046
Subject w. groups	15		
Time (B)	5.2	13.92	<0.001
AB	10.4	1.42	0.185
B x Subject w. groups	80		

Figure 1.   The effect of *Anax imperator* (caged and uncaged) on the number of egg rafts oviposited by *Culiseta longiareolata*. Error bars are ±1 standard error.

($F_{2,14}$=2.59, p=0.11) (Figure 4a). *Heterocypris* densities were not affected by the treatments ($F_{2,14}$=1.52, p=0.253) (Figure 4b).

Consistent with the trophic cascade hypothesis in a tritrophic system, periphyton mass was significantly higher in free *Anax* pools compared to control pools ($F_{2,15}$=2.92; p=0.042, one-tailed test because of *a priori* prediction) (Figure 5a). Evidence for a behavioral trophic cascade, i.e., higher periphyton densities in caged *Anax* pools compared to control pools, was not substantiated. Phytoplankton mass tended to be highest in the control pools though there were no significant differences ($F_{2,15}$=2.75; p=0.096; Fig. 5b).

DISCUSSION

An examination of differences between the control pools and free-*Anax* pools yields the overall (consumptive plus nonconsumptive) effect of *Anax* on densities of particular taxa. Free *Anax* strongly reduced *Culiseta* larval populations and virtually eliminated adult emergence for this species. This is an important impact since *Culiseta* immatures are the numerically dominant insect in desert temporary pools (Dimentman and Margalit 1981) and the dominant macroinvertebrate in pools within wadis (seasonal, intermittent streams) subject to flash floods (Blaustein and Margalit 1995, Ward and Blaustein 1994). They are not only numerically dominant, but appear to be important themselves in structuring the community. They were found to be influential intraguild predators of toad tadpoles (Blaustein and Margalit 1994a) and ceratopogonids (Blaustein and Margalit 1996) as well as strong competitors of toad tadpoles (Blaustein and Margalit

Table 2.   Repeated measures analysis of variance of the ln (x+1) of the number of *Culiseta longiareolata* in the different treatments on 9 dates from April 23 until June 14, for each class of *Culiseta*.

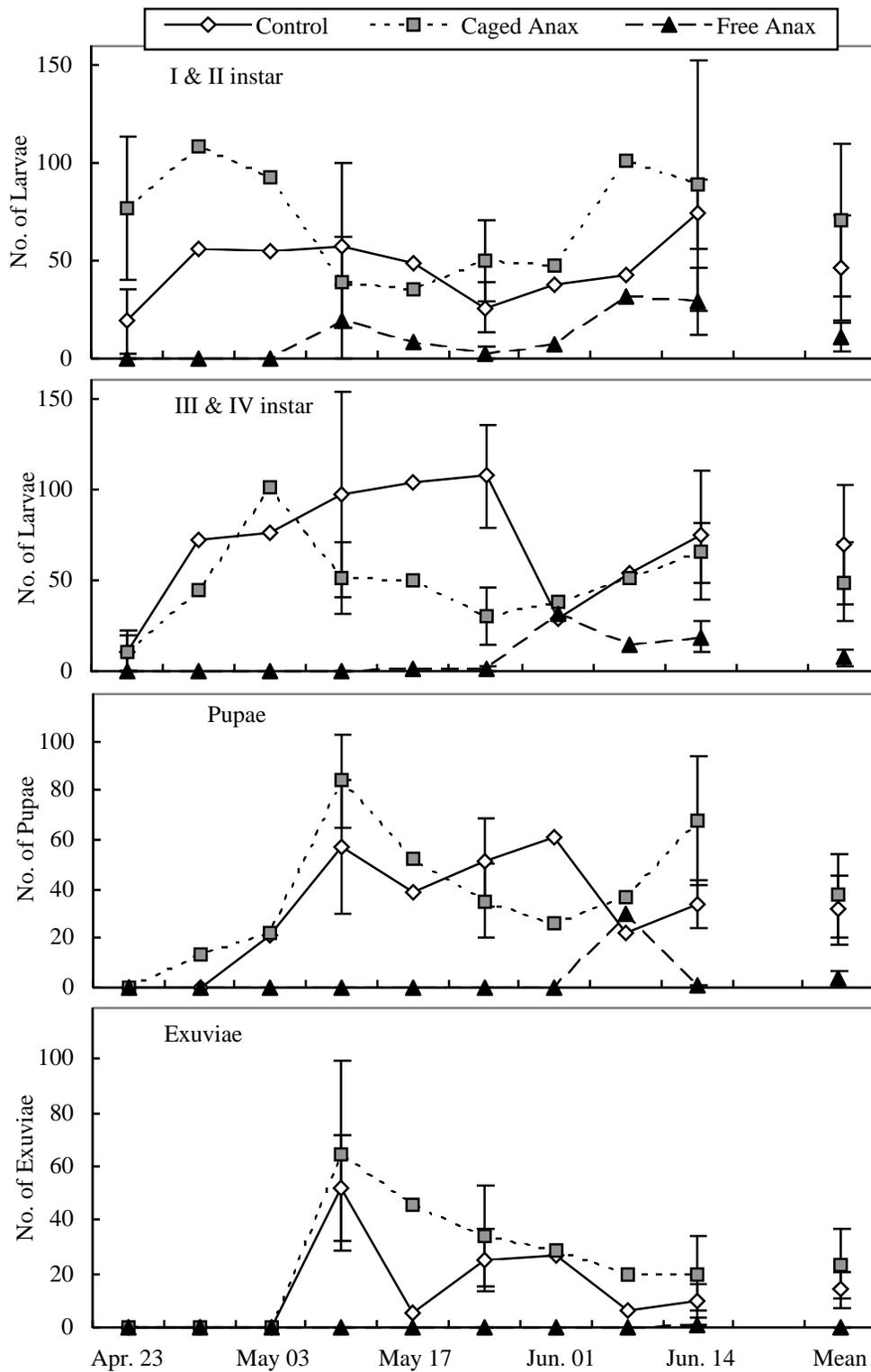| Instar	Treatment			Time			Treatment x Time		
	df	F	P	df	F	P	df	F	P
I and II	2,15	3.45	0.059	8,120	1.56	0.144	16,120	0.56	0.905
III and IV	2,15	8.30	0.004	8,120	6.61	<0.001	16,120	1.11	0.358
Pupae	2,15	10.22	0.002	8,120	6.64	<0.001	16,120	2.02	0.017
Exuviae	2,15	6.77	0.008	8,120	6.51	<0.001	16,120	2.21	0.008

Figure 2.　Effect of *Anax imperator* (caged and uncaged) on *Culiseta longiareolata*: (a) instar larvae I+II; (b) instar larvae III+IV; (c) pupae; (d) number emerging as adults (estimated by exuviae). Observations were made weekly from April 23 to June 14, 1996. The average results for each treatment for the entire period are presented on the right.

Table 3.   Repeated measures analysis of variance results for the effect of *Anax imperator* on the densities of chironomid pupal exuviae in the different treatments.

Source	df	F	P
Treatment (A)	2	1.34	0.293
Subject w. groups	15		
Time (B)	2	0.28	0.757
AB	4	0.70	0.600
B x subject w. groups	30		
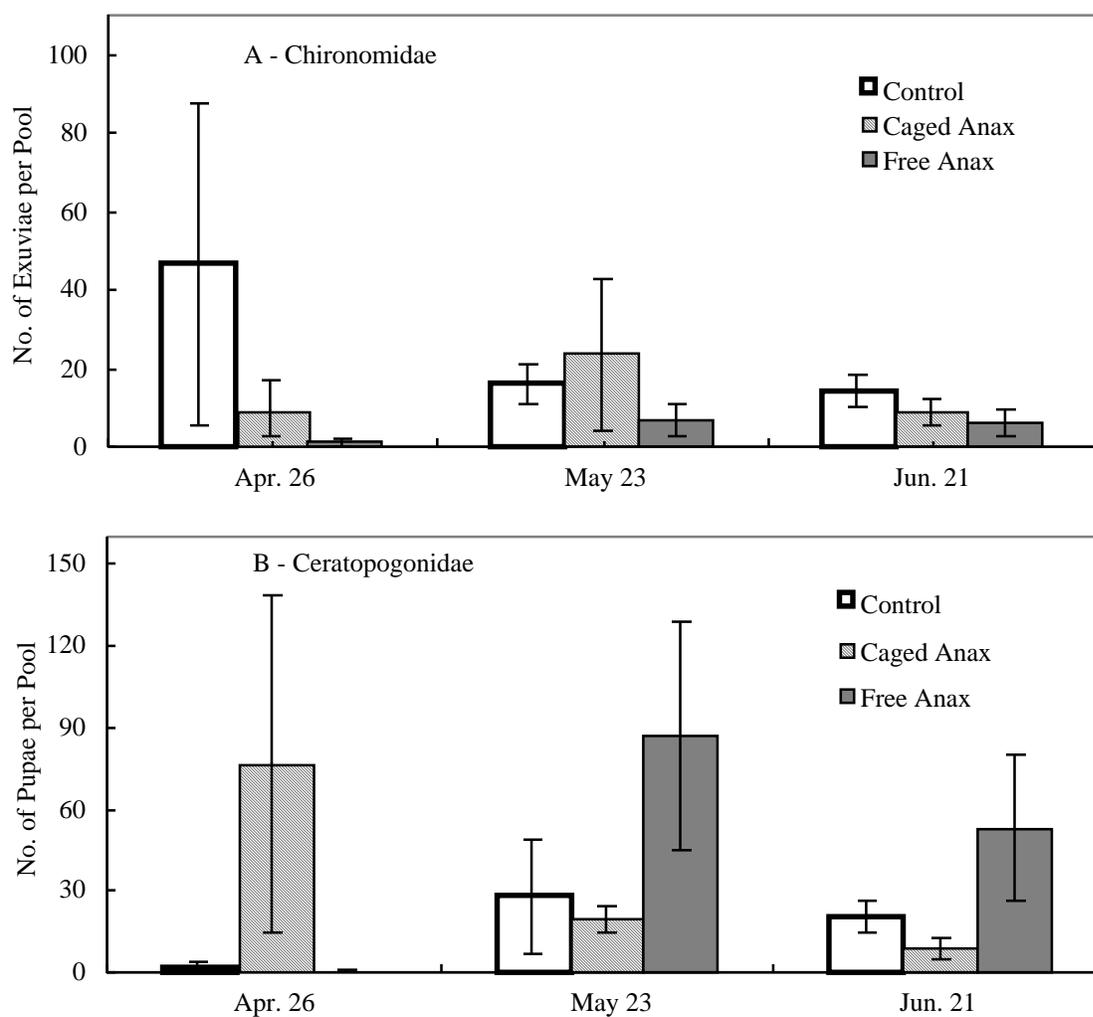
Figure 3.   Effect of *Anax imperator* (caged and uncaged) on: (a) number of chironomids emerging (exuviae); (b) ceratopogonid pupae. Error bars are ±1 standard error.

Table 4. Repeated measures analysis of variance results for the effect of *Anax imperator* on the densities of ceratopogonid pupae in the different treatments.

Source	df	F	P
Treatment (A)	2	0.54	0.596
Subject w. groups	15		
Time (B)	2	13.99	<0.001
AB	4	3.75	0.014
B x subject w. groups	30		
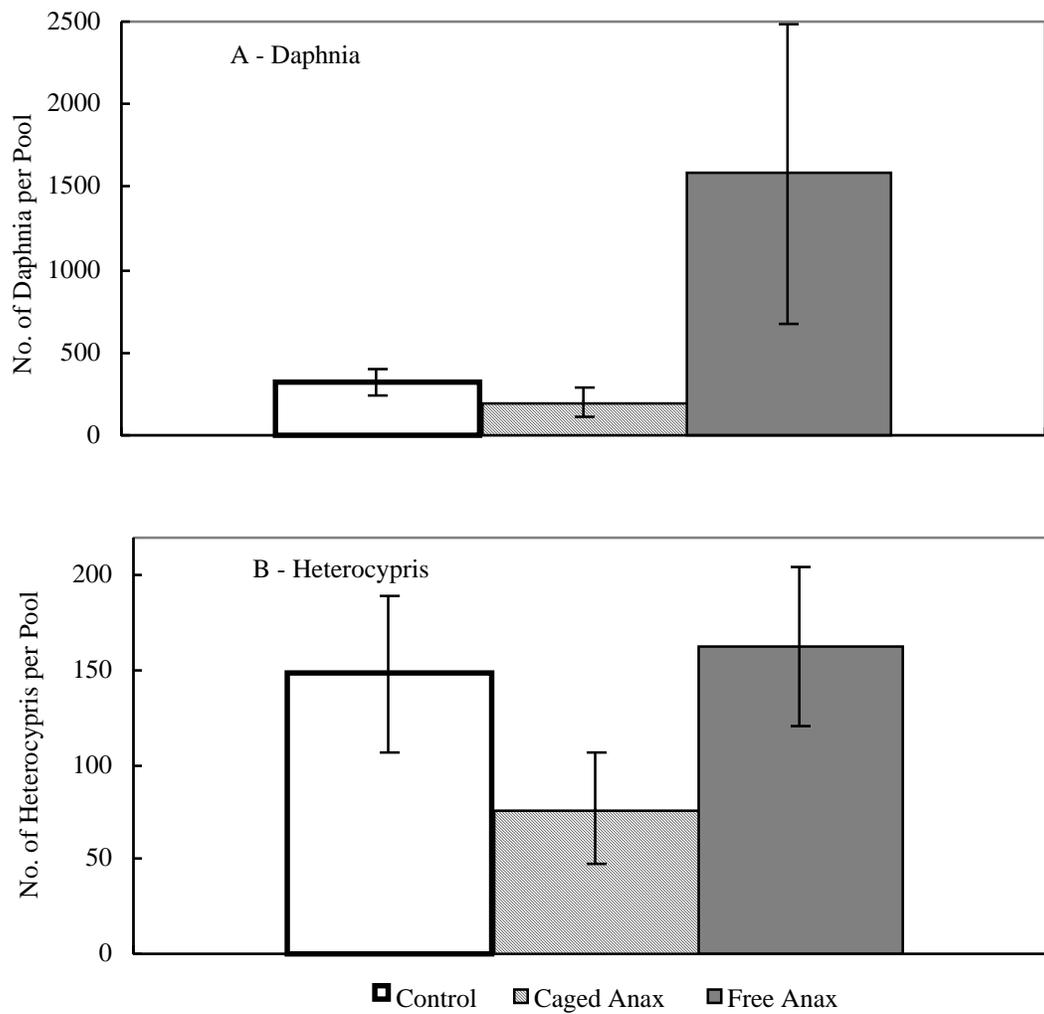
Figure 4. Effect of *Anax imperator* (caged and uncaged) on the two crustacean populations measured on 30 May 1996: (A) *Daphnia magna*; (B) *Heterocypris* sp. Error bars are ±1 standard error.

1994a). *Culiseta* is particularly vulnerable to a number of predators than, for example, *Culex* mosquitoes (Blaustein 1999). From an applied standpoint, the results here indicate that *Anax* can be an important natural control agent of mosquitoes, at least for those mosquitoes, such as *Culiseta* and many *Aedes* species that forage in open (exposed) microhabitats.

Anax did not reduce chironomid numbers. This is a somewhat surprising result in light of the fact that chironomids and *Anax* are both benthic and chironomid larvae are preyed upon readily by *Anax* in laboratory experiments (Blois-Heulin 1990). The lack of a negative direct effect of the predator on chironomid larvae (consumption) may be due to indirect positive effects. *Anax* virtually eliminated *Culiseta*, a predator of chironomid larvae and pupae (Blaustein, pers. obs.) and likely a competitor of chironomid larvae. Similarly,

Anax did not reduce another benthic taxon— ceratopogonids. If anything, densities were higher in the presence of *Anax* at the end of the experiment, although this might be because many of the *Anax* were emerging and/or preparing to emerge—many insects cease feeding prior to metamorphosis (Chapman 1969, Rockstein 1964). Again, the absence of an effect may be due to the drastic reduction of the intraguild predator, *Culiseta*.

We found it surprising that *Anax* did not reduce crustacean densities and possibly caused an increase in *Daphnia* densities. *Daphnia* was the primary source of food when maintaining *Anax* in the laboratory, and they readily fed on them. Although the possible positive effect of *Anax* on *Daphnia* densities was not significant (p=.11) , we have also conducted another experiment where a possible positive effect of *Anax* on *Daphnia*
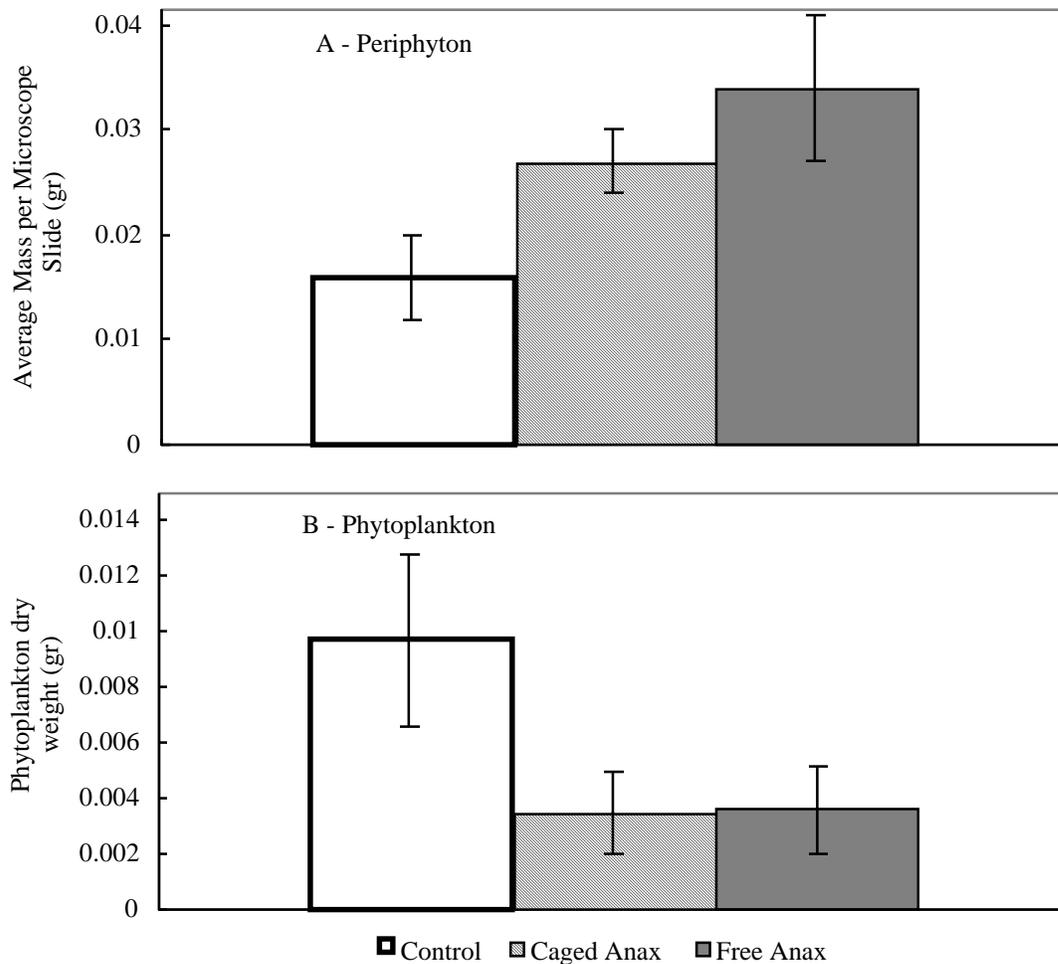

Figure 5.   Effect of *Anax imperator* (caged and uncaged) on (A) periphyton mass and (B) Phytoplankton dry weight.

densities also bordered on significance (Stav 1998). Nutrient regeneration caused by *Anax* predation on *Culiseta* and other organisms may possibly have caused an indirect positive effect or at least have negated consumption by *Anax*.

Strong (1992) suggested that good candidate systems for trophic cascades are ones that are low in both species richness and habitat heterogeneity. Temporary pools generally fit this description. *Anax* caused a trophic cascade, presumably because it strongly reduced *Culiseta* larvae, which are primarily periphyton grazers (van Pletsen 1981). This in turn allowed the periphyton mass to increase. It has been shown experimentally that *Culiseta* larvae reduced periphyton under similar conditions (Blaustein and Kotler, unpublished data) and that the predatory backswimmer, *Notonecta maculata*, caused a trophic cascade by virtually eliminating *Culiseta* larvae (Blaustein et al. 1995). Trophic cascades have also been demonstrated in artificial pool experiments where urodeles (Holomuzki et al. 1994, Morin 1995, Blaustein et al. 1996) were the top predators. Other experimental assessments have not shown evidence for a trophic cascade in pool habitats (Harris 1995).

A trophic cascade did not occur via the *Anax*-planktivore-phytoplankton pathway but this was not surprising because *Anax* did not reduce (and may possibly have increased) the predominant filter feeder, *Daphnia*. In contrast, *Notonecta* species have been shown to cause increases in phytoplankton (Koivisto et al. 1997, Arner et al. 1998, Blaustein et al. unpub. data).

A comparison of control pools and caged *Anax* pools should reveal non-consumptive effects of the predator. One such non-consumptive effect could be oviposition habitat selection in response to risk of predation. The reduction of *Culiseta* egg rafts in the free *Anax* treatment in a previous experiment (Stav et al. 1999) suggested to us that ovipositing *Culiseta* females might be able to assess risk of predation in a given pool and choose oviposition sites accordingly. Such a reduction was also found in *Culiseta* egg rafts in the presence of other predators: *Bufo* tadpoles (Blaustein and Kotler 1993), and *Notonecta* (Blaustein et al. 1995, Blaustein, 1998). A reduction of *Culiseta* egg rafts in caged *Anax* pools compared to control pools would have supported the hypothesis of predation risk sensitive oviposition instead of the alternative hypotheses of predation by *Anax* on ovipositing females or the egg rafts themselves. In this experiment, *Culiseta* did not demonstrate sensitivity to the risk of predation of the caged *Anax* when ovipositing. This does not entirely rule out the risk of predation hypothesis over the alternative hypotheses. It is possible that the cues

(kairomone, visual, or mechanical) could not be detected through the cage. Some aquatic animals respond to chemicals discharged from wounded conspecifics by avoiding the area (Howe and Sheikh 1975, Pfeiffer 1977, Sleeper et al. 1980, Hews and Blaustein 1985). Hews (1988) found that *Bufo boreas* tadpoles responded to chemical alarm and avoided the location where predation by the water bug *Lethocerus americanus* on conspecifics occurred. Such a mechanism may affect *Culiseta* females, and repel them from ovipositing in risky habitats. Caged *Anax* nymphs in this experiment were not fed on *Culiseta* immatures and thus possible chemical cues indicating predation on conspecifics could not occur. However, we have found that caged *Notonecta* induces avoidance by *Culiseta* females even when not fed with *Culiseta* (Blaustein, unpubl. data).

Alternative explanations to risk of predation are unlikely. We have shown experimentally that most or all of the reduction in the egg rafts cannot be attributed to predation on the egg rafts (Stav et al. 1999). Although we have not experimentally assessed whether *Anax* will prey upon ovipositing females, this is unlikely. First, *Anax* is a visual predator and preys during daylight hours (Blois-Heulin and Cloarec 1988), while *Culiseta* females oviposit at night. Secondly, *Anax* is largely a benthic predator, while *Culiseta* females stand motionless on the surface while laying their eggs. Moreover, we think it unlikely that *Anax* could visually detect ovipositing females or detect any vibrations, particularly since there were thousands of *Daphnia* in the water constantly swimming. With larger mesh and with a different predator (*Notonecta maculata*), Blaustein (unpubl. data) found that *Culiseta* responded as strongly to free *Notonecta* as they did to caged *Notonecta* demonstrating that at least for *Notonecta*, *Culiseta* females can detect risk of predation and oviposit accordingly.

Given that ovipositing *Culiseta* did not respond to caged *Anax*, we did not expect and did not find evidence for a behavioral trophic cascade. A behavioral trophic cascade may result if herbivores are less active (feed less) (Schmitz et al. 1997) or if there are fewer herbivores (oviposition habitat selection) in response to risk of predation. We did not measure prey activity here although casual observations did not reveal reduced activity in *Culiseta* larvae in response to *Anax* (Blaustein, pers. obs.). As caged *Anax* did not reduce the densities of *Culiseta*, or any other algal grazer or filter feeder, it is not surprising that there was not a behavioral trophic cascade. Had the mechanism for the trophic cascade been nutrient recycling by *Anax* rather than the reduction of herbivores; and thus herbivory, a trophic cascade,

might still be expected when comparing caged *Anax* to control pools. Thus, these results suggest that the mechanism for the trophic cascade is consumption (density reduction) of herbivores.

In summary, these results suggest that *Anax* has large impacts on *Culiseta* populations both through repelling oviposition and by consumption. It can also be an important organizer of temporary pool community structure. By virtually eliminating the dominant grazer *Culiseta*, it causes a trophic cascade with periphyton and likely reduces competition at the herbivore/detritivore level.

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