

## INDIVIDUAL AND INTERACTIVE EFFECTS OF A PREDATOR AND CONTROPHIC SPECIES ON MOSQUITO POPULATIONS

GIL STAV,<sup>1,2,3</sup> LEON BLAUSTEIN,<sup>2,4</sup> AND YOEL MARGALIT<sup>1</sup>

<sup>1</sup>Center of Biological Control, Department of Biology, Ben-Gurion University, Beer-Sheva 84105, Israel

<sup>2</sup>Laboratory of Community Ecology, Institute of Evolution, Faculty of Sciences, University of Haifa 31905, Israel

**Abstract.** Species sharing the same trophic level as mosquito larvae (hereafter, controphic species) may have complex effects on mosquitoes by sharing both predators and food resources. We conducted an outdoor artificial pool experiment to assess the individual and interactive effects of a predator (*Anax imperator*) and controphic species (primarily *Daphnia magna*) on larval populations of two common mosquitoes, *Culex pipiens* and *Culiseta longiareolata*.

Controphic species did not significantly affect survival to pupation of *C. pipiens* but did increase time to metamorphosis and reduce size at metamorphosis. *Culex pipiens* and *D. magna*, both primarily filter feeders, probably compete for food resources. Controphic species caused a small reduction (21.9%) in *C. longiareolata* survival, an unexpected result given that *C. longiareolata* larvae are thought to be primarily periphyton grazers while *D. magna* is a filter feeder. Controphic species did not affect *C. longiareolata* time to, or size at, pupation.

*Anax imperator* reduced *C. longiareolata* survival to pupation (78%) and size at pupation (11.5%) while increasing development time in males only (11.3%). *Anax imperator* caused a smaller (32.4%), but statistically significant, reduction in the number of *C. pipiens* surviving to the pupal stage but did not significantly affect size at or time to pupation. The predator did not reduce controphic species densities, and controphic species did not result in increased predator growth.

We predicted that controphic species, by serving as competitors, would result in fewer *C. pipiens* surviving to pupation in the absence of predators. In the presence of the predator, the negative competitive effect of controphic species would be attenuated by the positive effect of serving as alternative prey. Our results followed this pattern although the predator  $\times$  controphic species interaction was not statistically significant ( $P = 0.157$ ). Because previous studies showed that *D. magna* did not affect predation rates by *A. imperator* on *C. longiareolata* larvae, and because controphic species did not have a strong competitive effect, we did not predict and did not find a predator  $\times$  controphic species interactive effect.

**Key words:** *Anax imperator*; biological control; competition; controphic species; *Culex pipiens*; *Culiseta longiareolata*; *Daphnia magna*; interactive effects; mosquitoes; predation; trophic cascade.

### INTRODUCTION

Species sharing the same trophic level (hereafter, controphic species) may interact in complex ways. Those species sharing the same food resources should compete when resources are limiting. Competition is often important in structuring many communities (reviews by Connell 1983, Schoener 1983, 1993, Chase et al. 2002) including temporary pool communities (e.g., Scott 1990, Wilbur and Fauth 1990, Blaustein and Margalit 1994a, Mokany and Shine 2003).

Despite ecologists' understanding that competition is often a strong organizing force of communities, com-

petition between mosquitoes and controphic species such as zooplankton and anuran larvae has, surprisingly, been largely ignored as a potential regulating factor of mosquitoes. The handful of studies that have been conducted suggest that such controphic species are important competitors of larval mosquitoes (Blaustein and Karban 1990, Blaustein and Margalit 1994a, 1996, Chase and Knight 2003, Mokany and Shine 2003).

Sharing the same trophic level does not necessarily mean that diet overlap is high and that there is potential for resource competition. For example, many *Anopheles* and *Culex* mosquito larvae are primarily filter feeders, consuming phytoplankton and microzooplankton (such as protozoa) while many *Aedes* and *Culiseta* mosquito larvae are primarily periphyton feeders (Clements 1992). Since periphyton and phytoplankton may compete for nutrients (e.g., Axler and Reuter 1996), periphyton grazers may free up nutrients for phytoplankton and, conversely, phytoplankton grazers may free

Manuscript received 17 June 2003; revised 15 April 2004; accepted 19 May 2004; final version received 6 July 2004. Corresponding Editor: J. A. Logan.

<sup>3</sup> Present address: Department of Tropical Medicine, Tulane Health Sciences Center, 1430 Tulane Avenue, SL-17, New Orleans, Louisiana 70112.

<sup>4</sup> Corresponding author: E-mail: leon@research.haifa.ac.il

up nutrients for periphyton. Thus, controphic species that have low dietary overlap may be mutualists (e.g., McLachlan 1981, Bronmark et al. 1991, Heard 1994).

Controphic species often also share the same predators and thus serve as alternative prey. By serving as alternative prey, the immediate interaction of two controphic species may be mutualistic with each prey species reducing predation intensity on the other (Sih and Krupa 1996, Ackerman 2002, Ostman and Ives 2003). The influence of the alternative prey on predation may be influenced by the ratio of one prey species to its alternative prey; the greater the density of the alternative prey to the prey species in question, the more likely a greater reduction of predation intensity. It is also influenced by prey preferences. Prey preference may be further influenced by the relative abundance of different prey species; predators may "switch," feeding disproportionately more on abundant prey species and disproportionately less on rare species (Murdoch 1969, Lawton et al. 1974, Kimbrell and Holt 2004). Switching should have very important consequences for mosquito population dynamics; since mosquitoes often comprise a very small fraction of prey available to a generalist predator (e.g., Blaustein 1992), switching by predators would result in mosquitoes being preyed upon even less than at random.

While alternative prey will likely reduce predation intensity over the short term as shown in outdoor mesocosm (Wilbur and Fauth 1990) and laboratory (Chesson 1989, Blaustein 1990, Blaustein and Byard 1993) experiments, the effects may be the opposite over a longer term. Apparent competition (Holt 1977, Holt and Kotler 1987) may occur; because of the high density of the alternative prey's population, the predator may respond numerically (population growth) and developmentally (individual predators may grow faster). Thus, while two controphic species that share predators may initially have a mutualistic interaction, over a longer time scale predation intensity may increase, and the prey species should suffer more predation. In the case of mosquito control, such an effect has been suggested (e.g., Bence 1988, Blaustein 1992) but not experimentally assessed. It has been demonstrated in agricultural predator-pest systems (Karban et al. 1994, Ostman and Ives 2003).

Prey preference can also be influenced by prey size (Zaret 1980, Dillon 1985). Size-selective predation can strongly influence pool community structure (Sprules 1972, Blaustein et al. 1996). In many mosquito species, females are larger than males (Juliano and Stoffregen 1994, Lounibos et al. 1996, Hechtel and Juliano 1997). A size-selective predator may thus affect the sex ratio within a mosquito population. In addition, in many mosquito species, protandry occurs (i.e., males develop to adult faster [Barr 1985, Frank et al. 1985]). Thus, females of protandrous species may be at higher risk of being preyed upon by aquatic predators, both be-

cause they spend a longer time in the water and because they are larger.

The influence of a controphic species on another species includes not only the individual influences of competition and altered predation intensity, but also their combined effect. For example, a predator may act to mediate competition or coexistence (Paine 1966, Caswell 1978, Werner 1991, Chase et al. 2002). With rare exception (Chambers 1985), there has been almost no exploration of how a controphic species affects mosquito populations by sharing both resources and predators.

Irrespective of controphic species, predators can strongly influence mosquito populations via consumptive and nonconsumptive effects on mosquitoes themselves and on mosquitoes' resources. Amphibians, for example, typically display developmental plasticity by shortening time to metamorphosis and/or reducing size at metamorphosis when risk of predation is high (e.g., Werner and Anholt 1996). The mosquito *Ochlerotatus triseriatus* metamorphoses at a smaller size in the presence of a predator (Hechtel and Juliano 1997).

Predators can also indirectly influence community structure by causing a trophic cascade resulting in greater mass of the basal trophic level in tritrophic systems. This phenomenon, common in lake and pond systems (Leibold 1989, Carpenter and Kitchell 1993, Morin 1995), though varying greatly in strength (Brett and Goldman 1997, McCann et al. 1998), may have important consequences for mosquito success: predators in tritrophic pool ecosystems may indirectly benefit mosquitoes by providing more algal mass (i.e., food resources).

Temporary pools in deserts, being small simple systems with relatively low species diversity (e.g., Dimentman and Margalit 1981, Ward and Blaustein 1994), represent a convenient system to test the effects of predators and controphic species on mosquito populations. In the Negev and Dead Sea region deserts, pools not subject to the scouring effect of flash floods are often dominated by *Daphnia* species reaching densities of 1000s/L (G. Stav, *personal observation*). *Daphnia* are filter feeders. *Heterocypris* species (Ostracoda) can also become quite abundant (G. Stav, *personal observation*). *Culiseta longiareolata* Macquart and *Culex pipiens* L. are two common mosquitoes in these desert pools (Dimentman and Margalit 1981, Ward and Blaustein 1994). Filter-feeding mosquitoes such as *C. pipiens* could potentially compete with *Daphnia* for phytoplankton, bacterioplankton, microzooplankton, and particulate organic matter, while periphyton-grazing mosquitoes such as *C. longiareolata* may potentially compete with *Heterocypris*. As the rain pool season progresses, predators such as backswimmers and odonates can become abundant and can potentially have a large impact on mosquitoes. The role of backswimmers has been well studied (e.g., Blaustein et al. 1995, Blaustein 1998, Eitam et al. 2002), but

considerably less is known of the impacts of odonates in this system (Stav et al. 2000). Here, we determine experimentally, in outdoor artificial pools, individual and interactive effects of an odonate predator (*Anax imperator*) and controphic species of mosquito larvae (primarily *Daphnia magna*), on survival, time to and size at metamorphosis (pupation), as well as sex ratio of emerging adults of two mosquito species (*C. pipiens* and *C. longiareolata*).

#### METHODS

We established 20 plastic pools on the roof of the three-story Biology Department building, Ben-Gurion University (Beer-Sheva, Israel; 31°15' N, 34°48' E). Pools (34 × 59 cm on bottom, 25 cm in height, and 37 × 62 cm at water surface) were placed 0.5 m apart in a 4 × 5 grid. The size of these pools is well within the range of natural pools that contain the species of interest (Ward and Blaustein 1994, Blaustein and Margalit 1995). On 2 January 1995, we filled the pools to a depth of 20 cm (= 53 L) with tap water. Water levels were maintained by natural rains and distilled water. For a nutrient source, we added 5 cm<sup>3</sup> of ground food (30% Cat Lee cat food [no longer available]; 50% Koffolk mouse and rat chow [Koffolk, Tel Aviv, Israel]; 10% yeast; 10% Wardley Tropical fish flakes) on 9 January and then 2 cm<sup>3</sup> seven additional times weekly. On 13 February, to create a natural substrate, we added 1 L of loess soil collected at the water's edge of Zin Lake (a newly flooded body of water near the Dead Sea) to each pool. Prior to adding the soil to each pool, it was baked for 15 min after the soil center reached 80°C, with a final temperature of at least 100°C. At a height of 2 m we placed a net that provided 90% shade over the pools in order to reduce solar radiation since many natural pools had the natural shading of canyon walls and vegetation.

We employed a two-factor crossed design: (1) presence or absence of the predator, *A. imperator*; and (2) presence or absence of herbivores/detrivores, *D. magna* and *Heterocypris* species (controphic species). Each treatment combination was replicated in five randomly selected pools. To each appropriate pool, we added 100 *D. magna* on 9 January plus an additional 20 *D. magna* and 20 *Heterocypris* on 13 February.

On 7 March, we added two *A. imperator* nymphs (length =  $2.01 \pm 0.07$  cm [mean  $\pm$  1 SE]) to each appropriate pool. The introduction of *A. imperator* after the crustaceans simulates the natural phenology in temporary pools. Also on 7 March, we also added to all pools, 40 first instar *C. pipiens* larvae, collected as egg rafts in nearby natural pools. Once pupation began, we counted and removed pupae every day until no *C. pipiens* immatures remained (7 April). Early in the experiment, uncharacteristic larval mortality (100% or nearly 100%) occurred simultaneously in three adjacent pools of the three different predator/controphic species treatments. We suspected, but could not confirm, that

these pools were exposed to a mosquito-specific bacterial larvicide (*Bacillus thuringiensis israelensis*) that had been used in the immediate area (other species did not appear affected). At the time that this occurred, we decided to treat these pools as outliers and delete them from analysis. In addition, we also deleted the nearest control pool (which did not deviate from other control pools) to maintain a balanced design.

During the *C. pipiens* experiment, water temperatures ranged from 6°C to 30°C. We measured the thoracic length (end of wing pad to most distal edge) of each pupa. We then allowed pupae to emerge in the laboratory to determine gender of the adults. These data allowed us to assess the treatment effects on survival to pupal stage, size at pupation, rate of development, and sex ratio.

Four weeks after the termination of the *C. pipiens* experiment (5 May), we added 40 first instar *C. longiareolata* larvae (arising from egg rafts collected in nearby pools) to each pool. A phenology of *C. pipiens* followed by *C. longiareolata* was typically found in the Dead Sea region though there is high temporal overlap (Silberbush 2004). Given that the mosquito larval densities are lower than we might expect to see an intraspecific density-dependent effect (Blaustein and Margalit 1996), and that we waited approximately one month between the end of the *C. pipiens* and the beginning of the *C. longiareolata* experiments, we assume that there were no priority effects of the first mosquito on the second. The protocol for *C. longiareolata* was the same as for *C. pipiens* except that we counted and collected pupae every other day rather than every day. During the *C. longiareolata* experiment, water temperatures ranged from 14°C to 28°C.

Throughout the entire experiment, we removed mosquito egg rafts oviposited by wild mosquitoes to prevent the introduction of wild mosquito larvae. Oviposition data by wild mosquitoes are presented elsewhere (Stav et al. 1999).

On 3 May and 6 June, we surveyed for and measured the size of the dragonfly nymphs (total length). On 3 May, we found a missing or dead nymph in three pools and replaced them with live nymphs of similar sizes. On 7 April, 3 May, and 30 May, we sampled for controphic species with a 10.5 × 15.5 cm net (triangular shaped 0.11 mm<sup>2</sup> openings) sweeping a 6-L volume in each pool. On 3 May, we observed some *D. magna* in non controphic species pools, though in considerably lower numbers than in controphic species pools. After the *C. pipiens* experiment, we periodically swept all pools to remove *D. magna* from non-*D. magna* pools. *Daphnia magna* were removed from sweep contents in the non controphic species pools and then sweep contents were returned.

To measure periphyton, we used standard glass microscope slides (26 × 76 mm) vertically suspended at the center of the pools ~2 cm below the water surface. For the *C. pipiens* trial, we suspended one slide per

TABLE 1. Repeated-measures ANOVA results for  $\ln(x + 1)$  of the phytoplankton and periphyton mass.

Source of variation	df	Periphyton		Phytoplankton	
		F	P	F	P
Controphic spp. (C)	1	16.93	<0.001	2.33	0.147
Predator (P)	1	10.47	0.005	0.001	0.979
C $\times$ P	1	0.10	0.759	0.001	0.977
Subject within groups	16				
Time (T)	1	15.38	0.001	0.12	0.734
C $\times$ T	1	4.89	0.042	0.07	0.797
P $\times$ T	1	4.15	0.059	0.27	0.613
C $\times$ P $\times$ T	1	0.63	0.441	0.74	0.401
T $\times$ subject within groups	16				

pool on 20 March and collected them on 30 April. For the *C. longiareolata* trial, we suspended slides on 5 May and collected them on 29 May. We air dried slides in the laboratory for 48 h at 25°C. The material was then removed with a razor blade and weighed. On 30 April and again on 30 May, we measured the phytoplankton mass of a 50-mL water sample taken from each pool center at mid depth. Samples were filtered

through Whatman filter paper (qualitative 1) and dried at 80°C for 2 min before weighing.

Because many mosquito species show sexual dimorphism in size at, and time to, metamorphosis, we analyzed these variables separately for each sex. Data were analyzed as a two-way (controphic species and predator) analysis of variance (ANOVA). In the case of repeated measures over time, we used univariate

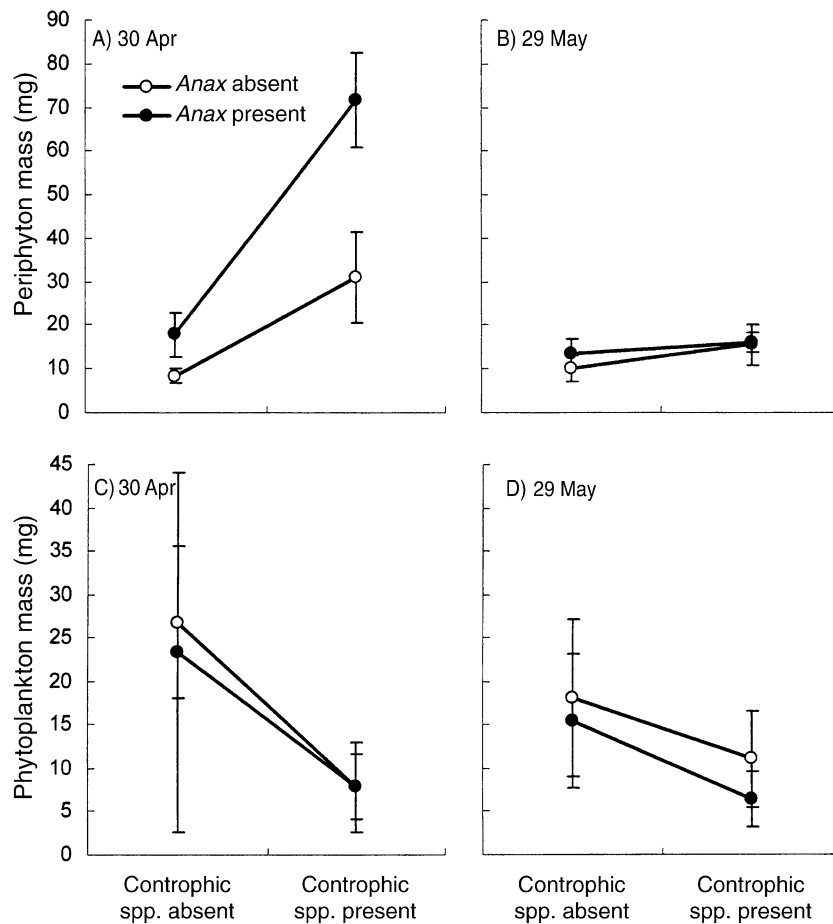


FIG. 1. The effects of controphic species and *Anax imperator* on mass (mean  $\pm$  1 SE) of phytoplankton and periphyton at the end of the *Culex pipiens* experiment (30 April 1995) and at the end of the *Culiseta longiareolata* experiment (29 May). For all panels, open circles are with *Anax* absent; filled circles are with *Anax* present.

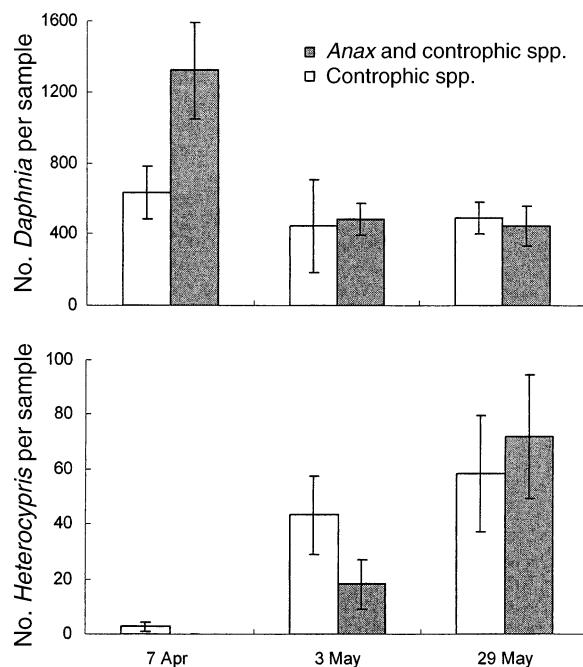


FIG. 2. Effects of *Anax imperator* on *Daphnia magna* (top) and *Heterocypris* sp. (bottom) densities per 6-L sample (mean  $\pm$  1 SE). Samples were taken on three dates: after the *Culex* period (7 April 1995), before *Culiseta longiareolata* larvae were added (3 May), and after the *Culiseta* period (29 May).

repeated-measures ANOVAs. Data were natural-log transformed ( $y + 1$ , when there were any zero values) prior to analysis when necessary to meet assumptions of ANOVA, which was the case for all analyses except for final survival to pupation for both species and for sex ratio, which was angularly transformed. During the *C. longiareolata* experiment, survival in one of the predator plus controphic species pools was uncharacteristically high (95% vs. a mean of 2% in the other four replicates). We classified this pool as an outlier for the *C. longiareolata* experiment based on both biological and statistical criteria. This lack of predation by *A. imperator* on *C. longiareolata* larvae is not only uncharacteristic of other replicates of this study (statistically significant outlier based on Grubb's test,  $P < 0.05$  [Sokal and Rohlf 1995]), but also uncharacteristic of other studies (Stav et al. 2000; L. Blaustein, un-

published data). Moreover, in the 6 June survey (one week after the termination of the *C. longiareolata* experiment), we found both of the *A. imperator* larvae missing from this pool.

## RESULTS

### Algae

*Anax imperator* caused an increase in periphyton mass ( $P = 0.005$ ; Table 1, Fig. 1a, b). This effect may have diminished in the second time period as suggested by the nearly significant predator  $\times$  time interaction ( $P = 0.059$ ). Controphic species also caused a significant increase in periphyton mass ( $P < 0.001$ ; Table 1, Fig. 1a, b). The effect of controphic species on periphyton diminished during the second sampling period as indicated by the significant controphic species  $\times$  time interaction ( $P = 0.042$ ).

No statistically significant treatment effects were demonstrated on phytoplankton mass (Table 1, Fig. 1c, d), though mass tended to be higher in the absence of controphic species (grand mean = 21.44 mg) than in its presence (grand mean = 10.47 mg,  $P = 0.147$ ).

### Controphic species and *Anax imperator*

The predator did not reduce crustacean densities (Fig. 2, Table 2). *Anax imperator* averaged  $2.01 \pm 0.07$  cm (mean  $\pm$  1 SE) total length when introduced on 7 March,  $3.57 \pm 0.06$  cm on 3 May, and  $3.80 \pm 0.04$  cm on 6 June. *Anax imperator* did not grow faster in the presence of the crustaceans ( $F_{1,8} = 0.55$ ,  $P = 0.480$ ).

### *Culex pipiens* experiment

The number of *C. pipiens* surviving to the pupal stage was significantly reduced (32.4%) by *A. imperator* ( $F_{1,12} = 5.84$ ,  $P = 0.033$ ), but was not significantly affected by controphic species ( $F_{1,12} = 0.18$ ,  $P = 0.680$ ; Fig. 3). Although *C. pipiens* tended to have higher survivorship in the presence of *A. imperator* plus controphic species pools compared to *A. Imperator* alone, the predator  $\times$  controphic species interaction was not statistically significant ( $F_{1,12} = 2.28$ ,  $P = 0.157$ ).

Because males pupated earlier than females, ANOVAs that considered mean time to pupation were considered separately for each sex. Both *C. pipiens* males ( $F_{1,12} = 23.81$ ,  $P < 0.001$ ) and females ( $F_{1,12} = 11.33$ ,

TABLE 2. Repeated-measures ANOVA results for  $\ln(x + 1)$  of the controphic species densities in the presence and absence of *Anax imperator*.

Source of variation	df	<i>Daphnia magna</i>		<i>Heterocypris</i> sp.	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<i>Anax</i>	1	2.24	0.173	0.21	0.979
Subject within groups	8				
Time	2	3.18	0.069	20.72	<0.001
<i>Anax</i> $\times$ time	2	0.95	0.408	2.24	0.139
Time $\times$ subject within groups	16				



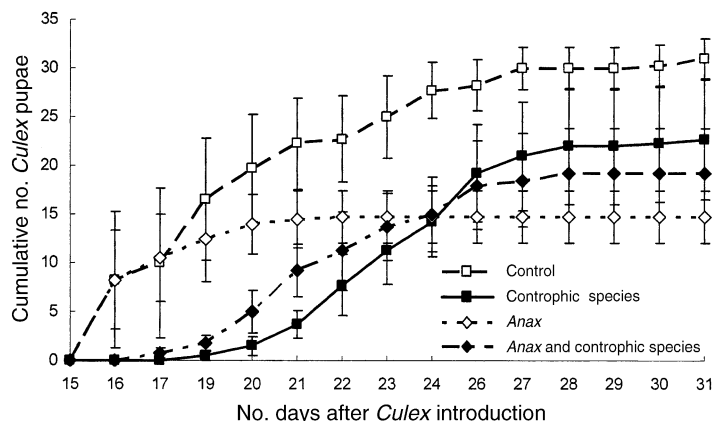


FIG. 3. The effects of the different treatments on cumulative survival to pupation of *Culex pipiens*. Error bars represent  $\pm 1$  SE.

$P = 0.006$ ) took longer to develop in the presence of controphic species (Fig. 4). Time to pupation also tended to be shorter in the presence of predators for both males ( $F_{1,12} = 3.93$ ,  $P = 0.071$ ) and females ( $F_{1,12} = 2.85$ ,  $P = 0.117$ ), though these differences were not statistically significant. The controphic species  $\times$  predator interaction was not statistically significant for either sex ( $P \gg 0.05$ ).

The repeated-measures ANOVA on cumulative number of *C. pipiens* pupae through time combines the effects of survival and pupation rate. This analysis showed a strong effect of controphic species ( $P = 0.015$ ; Table 3, Fig. 3). The highly significant controphic species  $\times$  time interaction ( $P < 0.001$ ) indicates that *C. pipiens* developed more slowly in the presence of controphic species, but by the end of the experiment controphic species did not affect the final number successfully pupating. The significant predator  $\times$  time interaction ( $P = 0.04$ ) indicates that pupation rate was high early in the experiment, but mortality was high for those that did not pupate early.

*Culex pipiens* male pupae were considerably smaller than female pupae (Fig. 5a). Controphic species caused a significant reduction in pupal size of *C. pipiens* males ( $F_{1,12} = 6.22$ ,  $P = 0.028$ ) and females ( $F_{1,12} = 10.90$ ,  $P = 0.006$ ; Fig. 5a). *Anax imperator* did not affect pupal size of either sex, nor was there a predator  $\times$  controphic species interaction for either sex ( $P \gg 0.05$  in all cases). However, both controphic species ( $F_{1,12} = 10.93$ ,  $P = 0.006$ ) and *A. imperator* ( $F_{1,12} = 6.90$ ,  $P = 0.022$ ) reduced the size differential between sexes (the male:female size ratio; Fig. 5b). These effects were additive (controphic species  $\times$  predator:  $F_{1,12} = 0.03$ ,  $P = 0.871$ ). The sex ratio of *C. pipiens* individuals reaching the pupal stage was not affected by either controphic species ( $F_{1,12} = 0.01$ ,  $P = 0.910$ ) or *A. imperator* ( $F_{1,12} = 3.00$ ,  $P = 0.109$ ).

#### *Culiseta longiareolata* experiment

The number of *C. longiareolata* surviving to the pupal stage was significantly reduced both by *A. imperator* (78%;  $F_{1,15} = 129.79$ ,  $P < 0.001$ ) and by con-

trrophic species (21.9%;  $F_{1,15} = 7.54$ ,  $P = 0.015$ ; Fig. 6). The combined effects of predator and controphic species did not deviate from additive (predator  $\times$  controphic species interaction:  $F_{1,15} = 0.37$ ,  $P = 0.554$ ).

Like *C. pipiens*, *C. longiareolata* males developed more quickly than females, and hence ANOVAs that considered mean time to pupation for each pool were considered separately for each sex. *Culiseta longiareolata* males ( $F_{1,14} = 5.00$ ,  $P = 0.042$ ), but not females ( $F_{1,13} = 0.83$ ,  $P = 0.379$ ), developed more slowly in the presence of *A. imperator* based on mean time to pupation (Fig. 7). Controphic species did not significantly affect mean time to pupation in either sex (males:  $F_{1,14} = 1.68$ ,  $P = 0.216$ ; females:  $F_{1,13} = 2.32$ ,  $P = 0.151$ ).

The repeated-measures ANOVA on cumulative number of pupae through time, which combines the effects on survival and pupation rate, showed that controphic species, and particularly *A. imperator*, had negative effects (Table 4, Fig. 6).

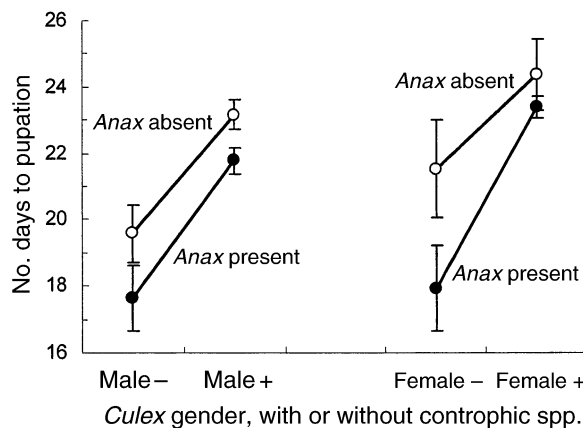


FIG. 4. The effects of the different treatments on time to metamorphosis (mean  $\pm 1$  SE) for *Culex pipiens*. In the x-axis labels, plus and minus symbols represent presence or absence of controphic species, respectively, for male vs. female *Culex*.

TABLE 3. Repeated-measures ANOVA results for the cumulative  $\ln(x + 1)$  of the *Culex pipiens* pupae in response to controphic species and/or *Anax imperator*.

Source of variation	df	MS	F	P
Controphic spp. (C)	1	31.89	8.11	0.015
Predator (P)	1	0.02	0.004	0.951
C $\times$ P	1	3.22	0.82	0.383
Subject within groups	12	3.93		
Time (T)	13	11.18	49.73	<0.001
C $\times$ T	13	1.77	7.89	<0.001
P $\times$ T	13	0.41	1.83	0.042
C $\times$ P $\times$ T	13	0.07	0.31	0.990
T $\times$ subject within groups	156	0.23		

*Anax imperator* caused a large reduction in *C. longiareolata* pupal size for both males ( $F_{1,14} = 13.93$ ,  $P = 0.002$ ) and females ( $F_{1,13} = 23.59$ ,  $P < 0.001$ ; Fig. 8). Controphic species did not influence size (males:  $F_{1,14} = 0.27$ ,  $P = 0.610$ ; females:  $F_{1,13} = 0.46$ ,  $P = 0.508$ ). Neither controphic species nor predator affected either the size ratio between the sexes or the sex ratios of emerging adults ( $P \gg 0.05$  in all cases).

#### DISCUSSION

Understanding how communities are organized may lend considerable insight into understanding the various and complex ways in which certain biotic components of communities influence mosquito populations. This, in turn, can help predict under what circumstances (i.e., specific community structures) a natural or introduced predator will successfully reduce mosquito populations. Here we assessed the importance of effects of a predator and controphic species on mosquito populations. Our results indicate that both of these components are important in influencing mosquito populations and that the effects on a particular mosquito species cannot be generalized across all mosquito species.

Controphic species caused *C. pipiens* larvae to develop more slowly and to pupate at a smaller size.

Reduced size at metamorphosis may have large negative consequences for mosquito fitness (e.g., Lounibos et al. 1993, Benjamin and Bradshaw 1994). Slower development rates should also decrease seasonal population growth. Among the controphic species, *D. magna* occurred in high densities and *Heterocypris* was found in only low densities during the *C. pipiens* experiment. *Daphnia magna* is competitively superior to many cladocerans species (e.g., Gliwicz 1990, Bengtsson 1993). Because both *C. pipiens* and *D. magna* are primarily filter feeders, these negative impacts of *D. magna* are most likely to be due to competition, presumably primarily exploitative. One common food source should be phytoplankton. Although the measured reduction of phytoplankton in the presence of controphic species was about two-thirds, the effect was not statistically significant. *Daphnia* species have reduced phytoplankton mass in a variety of lake and pond studies (e.g., Sarnelle 1992, Geist et al. 1993, Leibold and Wilbur 1993, Arner et al. 1998). Furthermore, the important limiting resource could have been edible, and not total, phytoplankton or some other microplankton or detritus that we did not measure.

This is the first experiment, to our knowledge, to show that *Culex* larvae compete with zooplankton and supports the circumstantial evidence of zooplankton

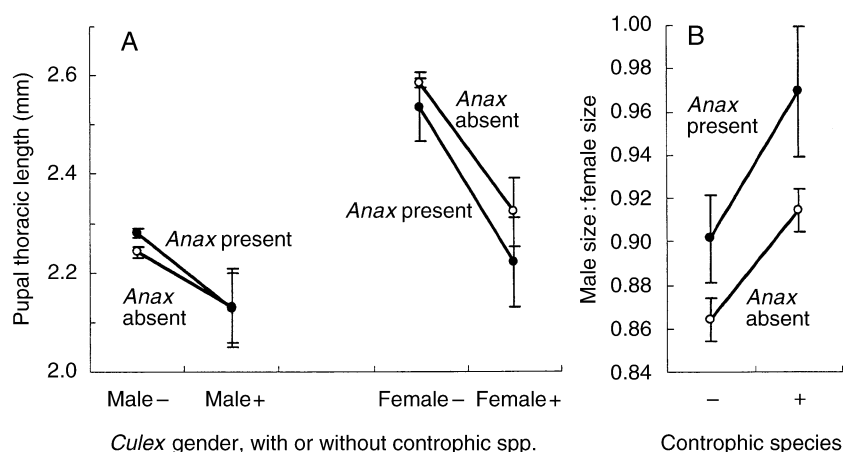


FIG. 5. The effects of controphic species and *Anax imperator* on (A) pupal size (thoracic length) of *Culex pipiens* and (B) the male : female thoracic length ratio. The plus and minus symbols in the x-axis labels represent presence or absence of controphic species, respectively. Error bars represent  $\pm 1$  SE.

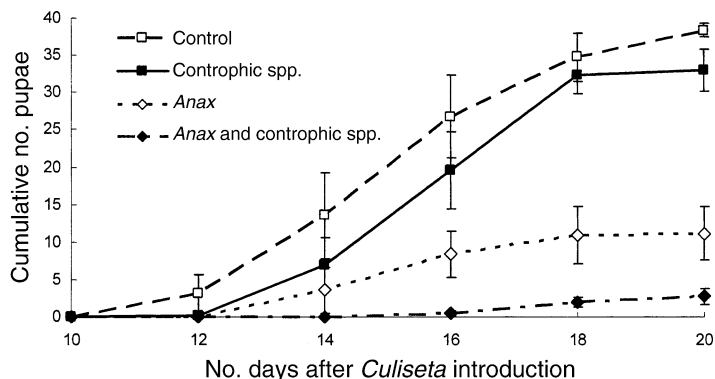


FIG. 6. Treatment effects on cumulative number of *Culiseta longiareolata* pupae (mean  $\pm$  1 SE).

competing with *Culex* larvae in rice fields (Blaustein and Karban 1990). Considering that *Daphnia* and other filter-feeding crustaceans are often orders of magnitude greater in abundance than mosquito larvae (e.g., Blaustein 1992), the effects of such controphic species in affecting population dynamics of some mosquito species may be very important.

*Culiseta longiareolata* larvae were also negatively influenced by the controphic species. Although *C. longiareolata* larvae and *D. magna* (the numerically dominant controphic species in our experiment) share the same trophic level, they may have little overlap in food; *C. longiareolata* has been reported to be primarily a periphyton grazer (van Pletsen and van der Linde 1981) while *D. magna* is a filter feeder. In fact, controphic species caused an increase in periphyton, possibly by reducing phytoplankton (potential competitors for sunlight and nutrients [Hansson 1992, Axler and Reuter 1996]) via grazing and re-releasing nutrients tied up in phytoplankton and animals to periphyton. One possible explanation is that *C. longiareolata* filter feeds more than is thought. A second possibility is that *D. magna* influence *C. longiareolata* via interference competition; we observed high densities of *D. magna* to result in frequent contacts with *C. longiareolata* causing the larvae to move. Lastly, *Heterocypris* sp., which grazes largely on periphyton (Pennak 1978), may have caused the negative effect. *Bufo viridis* tadpoles, which also feed largely on periphyton, have been shown to be strong competitors with *C. longiareolata* larvae in artificial pool experiments (Blaustein and Margalit 1994a, 1996).

*Anax imperator* had a large negative impact on *C. longiareolata* densities but a considerably smaller effect on *C. pipiens* densities. We cannot quantitatively compare the differences in the predation on the two mosquito species because the mosquitoes were introduced at different times with different conditions. For example, *A. imperator* nymphs were larger during the *C. longiareolata* experiment, and larger predators would be expected to have higher predation rates. However, this differential predation has also been observed in the laboratory: at depths as shallow as 6 cm and

with equal ratios of *Culex perixiguus* and *C. longiareolata* larvae, *A. imperator* fed almost exclusively on *C. longiareolata* (L. Blaustein, unpublished data). This is likely to be due largely to differences in behavior and body size between the two species. We have found (unpublished data) that *C. longiareolata*, compared to *C. pipiens*: (1) are more active, which attracts odonate larvae (Corbet 1980); (2) spend more time at the bottom where *A. imperator* are primarily found; and (3) are larger (Blaustein and Margalit 1994b) and *A. imperator* are size-selective predators preferring larger prey within the size range of mosquito larvae. Experimental evidence suggests that *C. longiareolata* females can detect *A. imperator* nymphs and avoid ovipositing in pools containing this predator (Stav et al. 1999). This oviposition response is not surprising in light of the heavy predation incurred by *C. longiareolata* larvae.

*Anax imperator* reduced development time in surviving males and pupal size in both sexes of *C. longiareolata*. Considerable work has shown that anuran tadpoles adjust development in response to risk of pre-

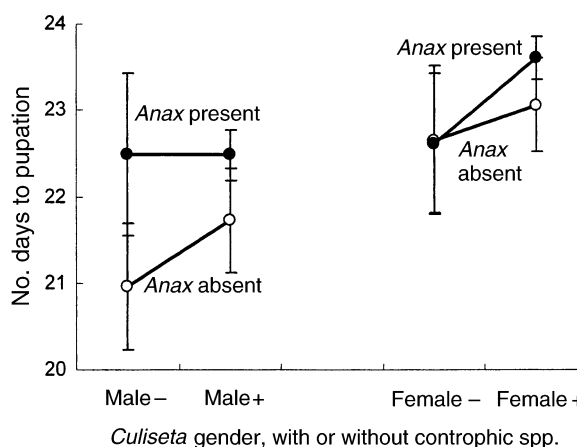


FIG. 7. The effects of controphic species and *Anax imperator* on *Culiseta longiareolata* time to metamorphosis (mean  $\pm$  1 SE). The plus and minus symbols in the x-axis labels represent presence or absence of controphic species, respectively.



TABLE 4. Repeated-measures ANOVA results for cumulative number of *Culiseta longiareolata* pupae in the different treatments.

Source of variation	df	MS	F	P
Controphic spp. (C)	1	664.68	4.52	0.051
Predator (P)	1	6732.17	45.74	<0.001
C $\times$ P	1	5.31	0.04	0.852
Subject within groups	15	147.19		
Time (T)	4	1472.63	59.39	<0.001
C $\times$ T	4	26.91	1.09	0.372
P $\times$ T	4	641.96	25.89	<0.001
C $\times$ P $\times$ T	4	22.28	0.90	0.471
T $\times$ subject within groups	60	24.80		

dation, including risk from congeneric *Anax* species (e.g., Skelly and Werner 1990, Werner and Anholt 1996, Trembath and Anholt 2001), though considerably less work has considered whether aquatic insect larvae possess such plasticity. As in the present study, Hechtel and Juliano (1997) found that the predator *Toxorhynchites* caused a decrease in pupal size of the mosquito *Aedes triseriatus*. Unlike this study, *Toxorhynchites* caused an increased time to pupation. The reduction in development time of *C. longiareolata* may not be due to developmental plasticity in response to risk of predation but rather those individuals taking longer to develop had an increased chance of being consumed.

Trophic cascades driven by backswimmers (Blaustein et al. 1995, Arner et al. 1998) and urodeles (Morin 1995, Blaustein et al. 1996) have been demonstrated in artificial pools. Predators may thus have indirect positive effects on mosquito larvae by increasing their food resource. *Anax imperator* did not cause a trophic cascade on phytoplankton (i.e., increased phytoplankton mass), though this might be explained by the fact that *A. imperator* did not reduce *D. magna*, the numerically dominant phytoplanktivore in the experimental community. *Anax imperator* did cause a trophic cascade on periphyton. The mechanism for this effect is unclear. The predator did not reduce densities of the

most abundant periphyton grazer (*Heterocypris*) and we used only low densities of the periphyton grazers, *C. longiareolata* larvae, which were present during only a small fraction of the entire study. Thus the most conventional mechanism of the predator reducing periphyton grazing by reducing grazer densities cannot explain the result. But there are at least two other potential mechanisms to bring about a trophic cascade. One is a behavioral trophic cascade (e.g., Schmitz and Suttle 1997) where *Heterocypris* would feed less in response to the predator. A second is nutrient regeneration by the predator (e.g., Peacor 2002). Our experimental design cannot differentiate between these.

How did *A. imperator* and the controphic species interact to affect mosquitoes? In the presence of controphic species, *A. imperator* did not grow faster. Thus, we should not expect, and did not find, apparent competition via a developmental response in *A. imperator* (i.e., controphic species presence did not cause an increase in consumption of mosquito larvae by *A. imperator*). Laboratory trials (G. Stav, unpublished data) show that *A. imperator* does not have a preference when offered *C. pipiens* and *D. magna*, indicating that the presence of *D. magna* should decrease predation intensity on *C. pipiens* larvae and thus increase survival. However, the fact that the controphic species reduces

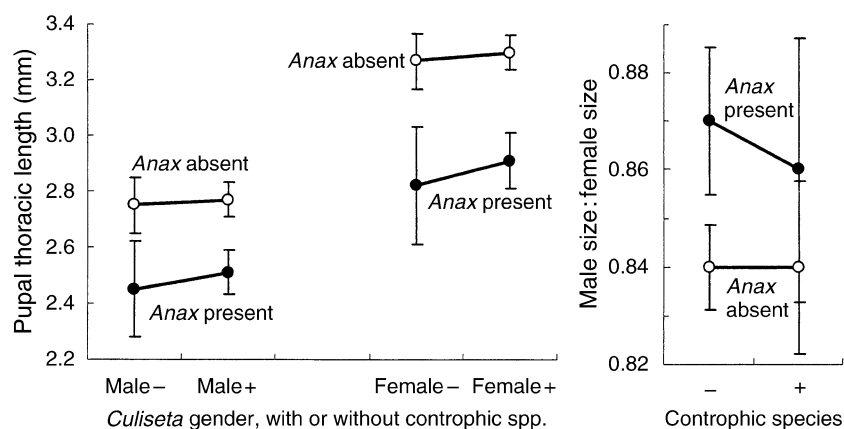


FIG. 8. The effects of controphic species and *Anax imperator* on (A) pupal size (thoracic length) and (B) the male : female thoracic length ratio of *Culiseta longiareolata*. The plus and minus symbols in the x-axis labels represent presence or absence of controphic species, respectively. Error bars represent  $\pm 1$  SE.

development rate (i.e., exposes *C. pipiens* to *A. imperator* predation for a longer period of time) should increase predation intensity. The absence of a statistically significant *A. imperator*  $\times$  controphic species interaction effect indicated that neither the negative competitive effect nor the positive alternative prey effect outweighs the other. Though the interaction was not statistically significant, the result was in the direction of the alternative prey effect being more important than the competitive effect.

Laboratory predation trials (G. Stav, *unpublished data*) showed that *A. imperator* strongly preferred *C. longiareolata* fourth instar larvae over adult *D. magna* (e.g., at equal ratios,  $72.9 \pm 13.8\%$  of the prey selected were *C. longiareolata* larvae). This laboratory study also showed no evidence of switching to the more abundant prey species. Given the strong preference for *C. longiareolata* larvae, it was not surprising that controphic species, by serving as alternative prey, did not influence the strong effect of predation. The negative effects of controphic species and predation tended to be additive.

These results indicate that *A. imperator* is an important predator of mosquitoes, particularly *C. longiareolata*. More importantly, this study demonstrates that species sharing the same trophic level as mosquitoes may strongly influence mosquito populations—either alone or interacting with predators. Very little work has thus far assessed the importance of these controphic species in affecting mosquito population dynamics. Our results indicate that their influence needs to be heavily considered in trying to understand the high among-site variability of mosquito abundance and the among-site variability in the success of predators to control mosquitoes.

#### ACKNOWLEDGMENTS

We thank Rakefet Stav and Perla Reides for technical help, Bert Schneider and Joel E. Cohen for enlightening discussions, and Burt P. Kotler, Zvika Abramsky, L. Philip Lounibos, and anonymous reviewers for critically reading and improving the paper. This research was supported by MERC USAID Grant 298.0158 awarded to Yoel Margalit and by United States–Israel Binational Science Foundation Grant 95-305 awarded to Leon Blaustein and Joel E. Cohen.

#### LITERATURE CITED

- Ackerman, J. T. 2002. Of mice and mallards: positive indirect effects of coexisting prey on waterfowl nest success. *Oikos* **99**:469–480.
- Arner, M., S. Koivisto, J. Norberg, and N. Kautsky. 1998. Trophic interaction in rockpool food webs: regulation of zooplankton and phytoplankton by *Notonecta* and *Daphnia*. *Freshwater Biology* **39**:79–90.
- Axler, R. P., and J. E. Reuter. 1996. Nitrate uptake by phytoplankton and periphyton: whole-lake enrichment and mesocosm-15N experiments in an oligotrophic lake. *Limnology and Oceanography* **41**:659–671.
- Barr, A. R. 1985. Population regulation of immature *Culiseta incidens*. Pages 147–154 in L. P. Lounibos, J. R. Rey, and J. H. Frank, editors. *Ecology of mosquitoes: proceedings of a workshop*. Florida Medical Entomology Laboratory, Vero Beach, Florida, USA.
- Bence, J. 1988. Indirect effects and biological control of mosquitoes by mosquitofish. *Journal of Applied Ecology* **25**:505–521.
- Bengtsson, J. 1993. Interspecific competition and determinants of extinction in experimental populations of three rockpool *Daphnia* species. *Oikos* **67**:451–464.
- Benjamin, S. N., and W. E. Bradshaw. 1994. Body size and flight activity effects on male reproductive success in the pitcher plant mosquito (Diptera: Culicidae). *Annals of the Entomological Society of America* **87**:331–336.
- Blaustein, L. 1990. Evidence for predatory flatworms as organizers of mosquito and zooplankton community structure in rice fields. *Hydrobiologia* **199**:179–191.
- Blaustein, L. 1992. Larvivorous fishes fail to control mosquitoes in experimental rice plots. *Hydrobiologia* **232**:219–232.
- Blaustein, L. 1998. Influence of the predatory backswimmer (*Notonecta maculata*) on invertebrate community structure. *Ecological Entomology* **23**:246–252.
- Blaustein, L., and R. Byard. 1993. Predation by a cyprinodontid fish, *Aphanius mento*, on *Culex pipiens*: effects of alternative prey and vegetation. *Journal of the American Mosquito Control Association* **9**:356–358.
- Blaustein, L., J. Friedman, and T. Fahima. 1996. Larval *Sal-amandra* drive temporary pool community dynamics: evidence from an artificial pool experiment. *Oikos* **76**:392–402.
- Blaustein, L., and R. Karban. 1990. Indirect effects of mosquitofish *Gambusia affinis* on the mosquito *Culex tarsalis*. *Limnology and Oceanography* **35**:767–771.
- Blaustein, L., B. P. Kotler, and D. Ward. 1995. Direct and indirect effects of a predatory backswimmer (*Notonecta maculata*) on community structure of desert temporary pools. *Ecological Entomology* **20**:311–318.
- Blaustein, L., and J. Margalit. 1994a. Mosquito larvae (*Culiseta longiareolata*) prey upon and compete with toad tadpoles (*Bufo viridis*). *Journal of Animal Ecology* **63**:841–850.
- Blaustein, L., and J. Margalit. 1994b. Differential vulnerability of species of mosquitoes to predation by the cyclopoid copepod, *Ancanthocyclops viridis*. *Israel Journal of Zoology* **40**:55–60.
- Blaustein, L., and J. Margalit. 1995. Spatial distributions of *Culiseta longiareolata* (Culicidae: Diptera) and *Bufo viridis* (Amphibia: Bufonidae) among and within desert pools. *Journal of Arid Environments* **29**:199–211.
- Blaustein, L., and J. Margalit. 1996. Priority effects in temporary pools: nature and outcome of mosquito larvae–toad tadpole interactions depend on order of entrance. *Journal of Animal Ecology* **65**:77–84.
- Brett, M. T., and C. R. Goldman. 1997. Consumer versus resource control in freshwater pelagic food webs. *Science* **275**:384–386.
- Bronmark, C., S. D. Rundle, and A. Erlandsson. 1991. Interactions between freshwater snails and tadpoles: competition and facilitation. *Oecologia* **87**:8–18.
- Carpenter, S. R., and J. F. Kitchell. 1993. *The trophic cascade in lakes*. Cambridge University press, Cambridge, UK.
- Caswell, H. 1978. Predator-mediated coexistence: a nonequilibrium model. *American Naturalist* **112**:127–154.
- Chambers, C. 1985. Competition and predation among larvae of three species of treehole-breeding mosquitoes. Pages 25–53 in L. P. Lounibos, J. R. Rey, and J. H. Frank, editors. *Ecology of mosquitoes: proceedings of a workshop*. Florida Medical Entomology Laboratory, Vero Beach, Florida, USA.
- Chase, J. M., P. A. Abrams, J. P. Grover, S. Diehl, P. Chesson, R. D. Holt, S. A. Richards, R. M. Nisbet, and T. J. Case. 2002. The interaction between predation and competition: a review and synthesis. *Ecology Letters* **5**:302–315.

- Chase, J. M., and T. M. Knight. 2003. Drought-induced mosquito outbreaks in wetlands. *Ecology Letters* **6**:1017–1024.
- Chesson, J. 1989. The effect of alternative prey on the functional response of *Notonecta hoffmani*. *Ecology* **70**:1227–1235.
- Clements, A. N. 1992. The biology of mosquitoes. Volume 1. Development, nutrition and reproduction. Chapman and Hall, London, UK.
- Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist* **122**:661–696.
- Corbet, P. S. 1980. Biology of Odonata. *Annual Review of Entomology* **25**:189–217.
- Dillon, M. P. 1985. Chironomid larval size and case presence influence capture success achieved by dragonfly larvae. *Freshwater Invertebrate Biology* **4**:22–29.
- Dimentman, C., and J. Margalit. 1981. Rain pools as breeding and dispersal sites of mosquitoes and other aquatic insects in the Central Negev Desert. *Journal of Arid Environments* **4**:123–129.
- Eitam, A., L. Blaustein, and M. Mangel. 2002. Effects of *Anisops sardea* (Hemiptera: Notonectidae) on oviposition habitat selection by mosquitoes and other dipterans and on community structure in artificial ponds. *Hydrobiologia* **485**:183–189.
- Frank, J. H., G. A. Curtis, and J. T. Rickard. 1985. Density-dependent sex ratio distortion and development bimodality in *Wyeomyia vanduzeei*. Pages 155–166 in L. P. Lounibos, J. R. Rey, and J. H. Frank, editors. *Ecology of mosquitoes: proceedings of a workshop*. Florida Medical Entomology Laboratory, Vero Beach, Florida, USA.
- Geist, D. R., A. T. Scholz, and R. A. Soltero. 1993. Relationship between phytoplankton volume and rainbow trout–*Daphnia pulex* interactions after phosphorus inactivation, Medical Lake, Washington. *Journal of Fresh Water Ecology* **8**:341–353.
- Gliwicz, Z. M. 1990. Food thresholds and body size in cladocerans. *Nature* **343**:638–640.
- Hansson, L. A. 1992. Factors regulating periphytic algal biomass. *Limnology and Oceanography* **37**:322–328.
- Heard, S. B. 1994. Pitcher-plant midges and mosquitoes: a processing chain commensalism. *Ecology* **75**:1647–1660.
- Hechtel, L. J., and S. A. Juliano. 1997. Effects of a predator on prey metamorphosis: plastic responses by prey or selective mortality? *Ecology* **78**:838–851.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* **12**:197–229.
- Holt, R. D., and B. P. Kotler. 1987. Short-term apparent competition. *American Naturalist* **130**:412–430.
- Juliano, S. A., and T. L. Stoffregen. 1994. Effects of habitat drying on size at time to metamorphosis in the tree hole mosquito *Aedes triseriatus*. *Oecologia* **97**:369–376.
- Karban, R., D. Hougén-Eitzmann, and G. English-Loeb. 1994. Predator-mediated competition between two herbivores that feed on grapevines. *Oecologia* **97**:508–511.
- Kimbrell, T., and R. D. Holt. 2004. On the interplay of predator switching and prey evasion in determining the stability of predator-prey dynamics. *Israel Journal of Zoology*, in press.
- Lawton, G. H., J. R. Beddington, and R. Bonser. 1974. Switching in invertebrate predators. Pages 141–158 in M. B. Usher and M. H. Williamson, editors. *Ecological stability*. Chapman and Hall, London, UK.
- Leibold, M. A. 1989. Resource edibility and the effect of predators and productivity on the outcome of trophic interactions. *American Naturalist* **134**:922–949.
- Leibold, M. A., and H. M. Wilbur. 1993. Interactions between food-web structure and nutrients on pond organisms. *Nature* **360**:341–343.
- Lounibos, L. P., R. L. Escher, D. Duzak, and E. A. Martin. 1996. Body size, sexual receptivity and larval cannibalism in relation to protandry among *Toxorhynchites* mosquitoes. *Oikos* **77**:309–316.
- Lounibos, L. P., N. Nishimura, and R. L. Escher. 1993. Fitness of treehole mosquito: influence of food type and predation. *Oikos* **66**:114–118.
- McCann, K. S., A. Hastings, and D. R. Strong. 1998. Trophic cascade and trophic trickles in pelagic food webs. *Proceedings of the Royal Society in London B* **265**:205–209.
- McLachlan, A. J. 1981. Interaction between insect larvae and tadpoles in tropical rain pools. *Ecological Entomology* **6**:175–181.
- Mokany, A., and R. Shine. 2003. Biological warfare in the garden pond: tadpoles suppress the growth of mosquito larvae. *Ecological Entomology* **28**:102–108.
- Morin, P. J. 1995. Functional redundancy, non-additive interaction, and supply-side dynamics in experimental pond communities. *Ecology* **76**:133–149.
- Murdoch, W. W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological Monographs* **39**:335–354.
- Ostman, O., and A. R. Ives. 2003. Scale-dependent interactions between two prey species through a shared predator. *Oikos* **102**:505–514.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* **100**:65–75.
- Peacor, S. D. 2002. Positive effect of predators on prey growth rate through induced modifications of prey behaviour. *Ecology Letters* **5**:77–85.
- Pennak, R. W. 1978. Fresh-water invertebrates of the United States. Second edition. John Wiley, New York, New York, USA.
- Sarnelle, O. 1992. Nutrient enrichment and grazer effects on phytoplankton in lakes. *Ecology* **73**:551–560.
- Schmitz, O. J., and K. B. Suttle. 1997. Effects of top predator species on direct and indirect interactions in a food web. *Ecology* **82**:2072–2081.
- Schoener, T. W. 1983. Field experiments on interspecific competition. *American Naturalist* **122**:240–285.
- Schoener, T. W. 1993. On the relative importance of direct vs. indirect effects in ecological communities. Pages 365–411 in H. Kawanabe, J. E. Cohen, and K. Iwasaki, editors. *Mutualism and community organization: behavioral, theoretical, and food-web approaches*. Oxford University Press, Oxford, UK.
- Scott, D. E. 1990. Effects of larval density in *Ambystoma opacum*: an experiment in large-scale field enclosures. *Ecology* **71**:296–306.
- Sih, A., and J. J. Krupa. 1996. Direct and indirect effects of multiple enemies on water strider mating dynamics. *Oecologia* **105**:179–188.
- Silberbush, A. 2004. Effects of salinity and predation on dipteran and algal temporary pool community structure: physiological and behavioral mechanisms. Dissertation. Ben Gurion University, Beer-Sheva, Israel.
- Skelly, D. K., and E. E. Werner. 1990. Behavioral and life-historical responses of larval American toads to an odonate predator. *Ecology* **71**:2313–2322.
- Sokal, R. F., and F. J. Rohlf. 1995. Biometry. Third edition. W.H. Freeman, New York, New York, USA.
- Sprules, W. G. 1972. Effects of size-selective predation and food competition on high altitude zooplankton communities. *Ecology* **53**:375–386.
- Stav, G., L. Blaustein, and J. Margalit. 1999. Experimental evidence for predation risk sensitive oviposition by mosquito, *Culiseta longiareolata*. *Ecological Entomology* **24**:202–207.
- Stav, G., L. Blaustein, and J. Margalit. 2000. Influence of nymphal *Anax imperator* (Odonata: Aeshnidae) on ovipo-

- sition by the mosquito *Culiseta longiareolata* (Diptera: Culicidae) and community structure in temporary pools. *Journal of Vector Ecology* **25**:190–202.
- Trembath, R., and B. R. Anholt. 2001. Predator induced morphological and behavioural changes in a temporary pool vertebrate. *Israel Journal of Zoology* **47**:419–431.
- van Pletsen, R., and T. C. van der Linde. 1981. Studies on the biology of *Culiseta longiareolata* (Macquart) (Diptera: Culicidae). *Bulletin of Entomological Research* **71**:71–79.
- Ward, D., and L. Blaustein. 1994. The overriding influence of flash floods on species-area curves in ephemeral Negev desert pools: a consideration of the value of island biogeography theory. *Journal of Biogeography* **21**:595–603.
- Werner, E. E. 1991. Nonlethal effects of a predator on competitive interactions between two anuran larvae. *Ecology* **72**:1709–1720.
- Werner, E. E., and B. R. Anholt. 1996. Predator-induced behavioral indirect effects: consequences to competitive interactions in anuran larvae. *Ecology* **77**:157–169.
- Wilbur, H. M., and J. E. Fauth. 1990. Experimental aquatic food webs: interactions between two predators and two prey. *American Naturalist* **135**:176–204.
- Zaret, T. 1980. *Predation and freshwater communities*. Yale University Press, New Haven, Connecticut, USA.