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Prey choice by a freshwater copepod on larval *Aedes* mosquitoes in the presence of alternative prey

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ABSTRACT: Predator-prey interactions can have a significant impact on the abundance and distribution of species, but the outcome of these interactions is often context-dependent. In small freshwater habitats, predacious copepods are potential biological control agents for mosquito larvae. Through laboratory experiments, we tested if the presence of a non-mosquito prey (neonate *Daphnia pulex)* influenced prey selection of the predaceous copepod (*Acanthocyclops vernalis*) on 1st instar *Aedes* mosquitoes (*Aedes aegypti* and *Aedes albopictus*). Copepods were starved for 12 h prior to being exposed to the two prey types (larval mosquitoes and *Daphnia)* at three densities: 25 mosquitoes:75 *Daphnia*, 50 mosquitoes:50 *Daphnia*, 75 mosquitoes:25 *Daphnia*. Single prey choice trials for each species as well as no-predator trials were also established for controls. Copepods were effective predators, with a single copepod consuming up to 37 1st instar mosquito larvae during the 24-h trials. The number of mosquitoes consumed increased with their relative density, but the proportion of mosquitoes consumed was highest when *Aedes* made up only 25% of the population. Results from our study show that in a simple predator/two-prey system, two species of larval mosquitoes (*Ae. aegypti* and *Ae. albopictus*) are preferentially consumed over an alternative zooplankton by the copepod predator *Acanthocyclops vernalis.* ***Journal of Vector Ecology*** **46 (2): 200-206. 2021.**

Keyword Index: Mosquitoes, zooplankton, biocontrol, predator-prey interactions, predator behavior, alternative prey hypothesis.

INTRODUCTION

Predator-prey interactions have long been known to influence the abundance and distribution of species (Sih et al. 1985, Kitchell et al. 1994, Gilg et al. 2009). However, other members of the community often influence predator-prey interactions between two species (Spitze 1992, Vik et al. 2008, Masoero et al. 2020). For example, in multi-prey systems, the presence of alternative prey may prompt a predator to switch consumption to a higher-density prey when the density of its focal prey is low (i.e., prey switching). This prey switching may offer low-density refuge for target prey and facilitate coexistence among prey taxa (but see Pöysä et al. 2016). The outcomes of these interactions are often context-dependent, making it difficult to generalize predictions among systems (Prokopenko et al. 2017, Schmitz 2017, Cuthbert et al. 2020a). In situations where biocontrol of the target species is the intended outcome, an accurate knowledge of predation rates in the presence of alternative prey is essential.

Temporary freshwater habitats are ubiquitous and diverse systems, often hosting several species of zooplankton and insects, including predators and larval mosquitoes (Scheffer et al. 2006, Holmes and Cáceres 2020). Controlling larval mosquitoes in these systems has received considerable attention given the ability of adult mosquitoes to transmit a number of disease-causing agents to humans (Calliari et al. 2003, Benelli et al. 2016). Large-bodied copepods, such as those in the genera *Mesocyclops* and *Acanthocyclops,* can be among the most common and effective predators in these temporary systems (Schreiber et al. 1996, Marten et al. 1994, 2000b, Kumar and Hwang 2005, Benelli et al. 2016).

Though laboratory experiments have demonstrated copepods to be effective predators of mosquitoes, these studies often lack the diverse and complex food webs often found in these natural systems. Zooplankton and macroinvertebrates can deter predators from consuming mosquito larvae (Blaustein and Chase 2007). Hence, studies examining the effects of alternative prey on mosquito consumption are necessary to understand the effectiveness of this potential biological control agent.

We conducted a laboratory experiment to determine if the presence of alternative prey influenced patterns of prey consumption for the predatory copepod (*Acanthocyclops vernalis*). *Acanthocyclops* copepods are well-documented predators of freshwater invertebrates and are known to influence the populations of zooplankton and larval mosquitoes through their selective consumption behavior (Nasci et al. 1987, Marten 1989, 1990a, Marten et al. 2000b, Enríquez-García et al. 2013, Alshammari et al. 2015, Sarma et al. 2019). In our experiment, we varied relative prey density of *Daphnia pulex* and mosquito larvae (*Aedes albopictus* or *Aedes aegypti*) and measured consumption by the predator *A. vernalis* after 24-h laboratory trials.

MATERIALS AND METHODS

Collection and maintenance of predators and prey

Copepods (*Acanthocyclops vernalis*) were collected from a local retention pond (40°06'30.9"N 88°10'38.2"W). Large-bodied copepods suspected to be *A. vernalis* were isolated in

200 ml of filtered pond water and were fed lab-raised *Daphnia* until the start of the experiment. Following predator-prey trials, the copepods were preserved in 95% EtOH and dissected for identification using Haney et al. (An-Image-based Key to the Zooplankton of North America, version 5.0. 2013. http://www.cfb.unh.edu). Trials with copepods that could not be confidently identified as *A. vernalis* were excluded from all analyses presented herein.

Our mosquito prey were 1st instar (<12 h old) larvae of *Aedes albopictus* and *Aedes aegypti* collected from eggs hatched from colonies at the Medical Entomology Laboratory at the Illinois Natural History Survey. Details on mosquito colony maintenance can be found in Parker et al. (2019). First instar individuals were selected, as previous studies have shown predators avoid later-stage larval mosquito instars (Brown et al. 1991, Tranchida et al. 2009). Eggs from laboratory-reared adults were preserved on damp germination paper and kept in a 15° C cold room until hatching. To induce hatching, mosquito eggs were first conditioned at room temperature for 48 h. Eggs were then submerged in a Brain Heart Infusion (BHI) broth solution for 24 h at 27° C and checked regularly for hatching.

The freshwater zooplankter *Daphnia pulex* was selected as the alternative prey as it commonly inhabits small freshwater ponds and often co-occurs with larval mosquitoes (Holmes et al. 2016). All *D. pulex* were batch-cultured, fed high-quantity and quality algae prior to the start of the experiment. We selected only < 48-h neonate *Daphnia* for use in prey selectivity experiments to ensure both prey types were similar in size.

Experimental predator-prey trials

We examined the extent to which availability of alternative prey influences consumption by the predatory copepod, *A. vernalis*. In a laboratory experiment, a single predator was exposed to both mosquito and *Daphnia* prey at different relative densities. Consumption of prey was measured after 24 h across the density gradient. Experimental trials were conducted in a 100 ml mixture of pond and lake water using a 75/25 ml ratio (lake/pond). This ratio was used as we found it favorable to the viability of prey in the absence of predators. Trials were run separately for the two mosquito species. We varied the abundance of 1st instar mosquito larvae (*Ae. albopictus* or *Ae. aegypti*) and *D. pulex* prey in the following ratios (mosquito: *Daphnia*): 0:100, 25:75, 50:50, 75:25, 100:0, such that total prey abundance was always 100 individuals. We used this high density of prey to ensure the predator had adequate access to prey. Each density treatment was replicated six times, but our final sample size ranged from four to six due to premature predator mortality and issues with sample preservation. We included a no-predator control, to determine baseline mortality of the prey used in this study (n=3 per mosquito species).

For the trials, a single *Acanthocyclops vernalis* copepod was added to a beaker containing 100 ml of filtered lake water and was starved for approximately 12-16 h (at 19-21° C) prior to prey introductions. To ensure all treatments were inoculated within five min of one another, prey were pre-counted and sorted to holding beakers until inoculations. Prey stocking inoculums were re-counted immediately prior to being added to experimental beakers. Following inoculation, all experimental beakers were held at 21° C for approximately 24 h. Immediately following the 24-h trials, all animals were filtered through an 80 µm sieve and preserved in 95% EtOH until samples were counted. Any partially consumed prey were counted as prey consumed. For the no-predator controls, the two prey types were introduced in an equal ratio (50:50) and kept in the same experimental conditions as treatments (24-h period, 100 ml water mixture).

Statistical analyses

All analyses were conducted in SAS version 9.4 (SAS 9.4, Cary, NC. SAS Institute Inc.). To determine the efficacy of *Acanthocyclops* copepods as potential biocontrol agents in the presence of alternative prey, we conducted five analyses. First, to examine differences in predation rate when only a single prey item is offered, we conducted a one-way ANOVA with prey type (*Ae. aegypti*, *Ae. albopictus*, and *D. pulex*) as the main factor and number of individuals consumed as the response variable. We used both a two-way ANOVA and multivariate logistic ANOVA to assess differences in numbers of consumed prey across multi-prey density treatments (25, 50, 75 mosquitoes) and mosquito species (*Ae. albopictus* and *Ae. aegypti*). The logistic ANOVA was run using Proc GENMOD, where every mosquito was scored as either alive or dead at the end of the trial. This analysis also included the 100% mosquito treatment for comparison.

Predator preference was evaluated through the Manly-Chesson selectivity index (α: (Manly 1974, Chesson 1978, 1983):

$$\alpha = \frac{(r_i/p_i)}{\sum(r_i/p_i)} \qquad i = 1,2, \ldots .m$$

where r_i = proportion of prey item found in diet, p_i = proportion of food item in the environment, and m = the total number of food items in the environment. The threshold for random feeding in predators is equal to $1/m$ (number of prey types); with two prey types the threshold is 0.5. Any value that is significantly above 0.5 indicates positive selection. We conducted a one-sample t-test to determine whether mean selectivity (α) for each mosquito species differed from the threshold of no-prey selectivity (0.5). Any significant deviation from 0.5 suggests that *Acanthocyclops* copepods preferentially consumed (>0.5) or actively avoided consuming (<0.5) larval mosquitoes. Finally, we used a two-way ANOVA to determine how Manly-Chesson α varied between density (25%, 50%, 75%) and mosquito species (*Ae. albopictus* and *Ae. aegypti*) treatments.

RESULTS

Survivorship of *Daphnia* and both species of mosquitoes was high in the predator-free controls (*Ae. aegypti* – 97%, *Ae. albopictus* – 96%, *Daphnia* – 96%), indicating that the much higher loss rates in the presence of *Acanthocyclops* copepods was the result of predation.

When presented with 100 individuals of a single prey item, a single *Acanthocyclops* copepod consumed an average of 45 *Daphnia*, 28 *Ae. albopictus*, and 25 *Ae. aegypti* in 24 h (Figure 1A). However, individual variation in predator behavior, especially when isolated with *Daphnia*, resulted in no difference in consumption rate among the three single-prey items ($F_{2,13}$ = 1.6, P = 0.22). In the mixed prey species trials, total prey consumption ranged from 10 to 71 individuals (average 26 ± 2.6, Figure 1B).

When exposed to both prey types, *Acanthocyclops* copepods consumed similar total amounts of prey when compared to the single-prey trials (27.1% ± 2.4% of total prey). A two-way ANOVA with number of mosquitoes (25, 50, or 75) and mosquito species (*Ae. aegypti* or *Ae. albopictus*) as factors showed that there was no difference in the total number of prey individuals consumed by *Acanthocyclops* copepods regardless of the relative density ($F_{2,25}$ = 2.9, P = 0.07) or species ($F_{1,25}$ = 0.001, P = 0.99; Figure 1B).

When exposed to both prey types, the percentage of mosquitoes consumed peaked at a mosquito density of 25% for both species (44% ± 5.6% for *Ae. aegypti*; 44% ± 2.8% for *Ae. albopictus*). Fewer mosquitoes were consumed for higher initial mosquito densities. When exposed to mosquitoes in isolation, the percentage of mosquitoes consumed was higher than the 75% mosquito treatment but not to the same extent as the 25% treatment. A logistic ANOVA revealed no difference in percent consumed between species ($\mathcal{X}^2$ = 0.50, P = 0.48), but a significant difference between treatments ($\mathcal{X}^2$ = 50.39, P < 0.0001, Figure 3A).

Individual predators exhibited variation in the strength of prey selectivity; Manly-Chesson α ranged from 0.26 to 0.88 in *Ae. aegypti* and 0.35 to 0.85 in *Ae. albopictus* (Figure 2). Despite this variation, there was evidence that when given the choice, *Acanthocyclops* copepods preferred both *Ae. aegypti* (t-test, t = 2.81, df = 14, P = 0.01) and *Ae. albopictus* (t-test, t = 2.59, df =15, P = 0.02) over *Daphnia* (Figure 2). However, Manly-Chesson α did not differ between mosquito species ($F_{1,25}$ = 0.36, P = 0.55; Figure 3B) or across relative prey density treatments ($F_{2,25}$ = 0.15, P = 0.86; Figure 3B).

DISCUSSION

Acanthocyclops vernalis is an effective predator on 1st instar larval *Aedes*, regardless of the density of alternative prey. A single copepod can consume more than 30 larvae in 24 h. Our findings are comparable to other studies that observed consumption rates of 20 1st and 2nd instar larvae (Alshammari et al. 2015) and 33 1st instar larvae (Marten 1990a) per 24-h period. Not surprisingly, we found that as the number of mosquitoes in the containers increased, more individuals were consumed. However, the greatest proportion of mosquitoes was consumed in the treatment with the fewest mosquitoes (25%: 25 larvae and 75 *Daphnia)*. In our study, *A. vernalis* copepods preferentially consumed *Aedes* larvae even in the presence of alternative prey in varying densities (*Daphnia*). This prey preference, in addition to the consumption of a high proportion of mosquitoes in low density conditions, are ideal features of potential biocontrol agents and should be further explored in greater detail for these and other mosquito species. Nevertheless, we found considerable individual variation in predator behavior, which may result in a wide range of consumption patterns in practice.

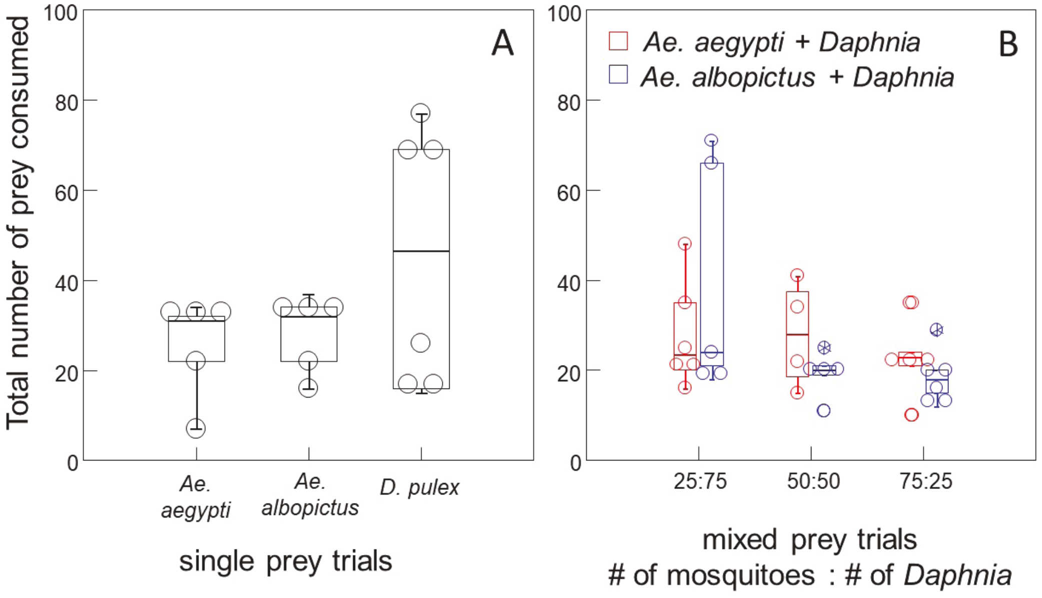

Figure 1: Total number of prey consumed by *Acanthocyclop*s in single and mixed prey trials. A) In single prey trials, there was no difference in consumption between the prey types with, on average, 30-40 prey items (out of 100) being consumed. B) In trials with mixed diets (25:75, 50:50, 75:25, mosquitoes: *Daphnia*), on average 26 total prey items were consumed, with no difference among treatments. Asterisks indicate extreme data points (points that exceed three box lengths from the median).

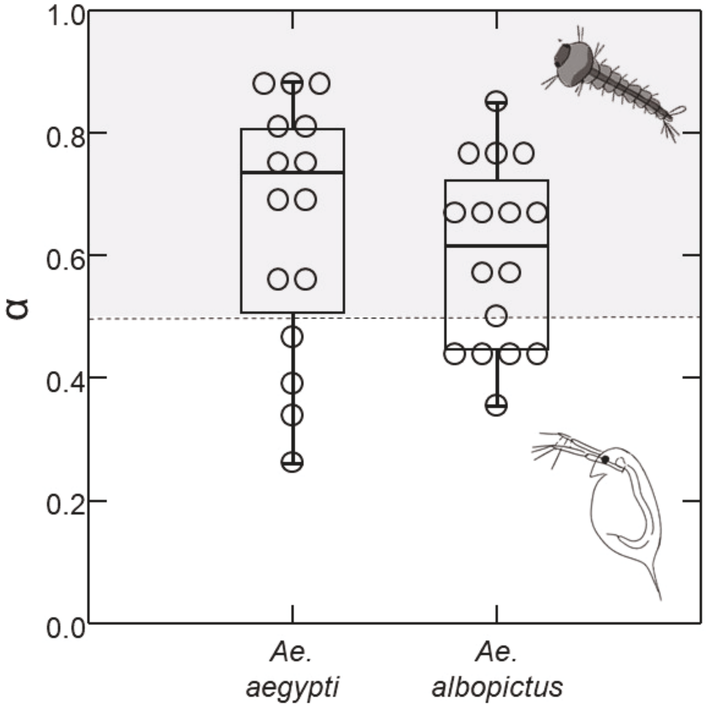

Figure 2. Manly-Chesson α for *Acanthocyclops* presented with either Ae. aegypti or *Ae. albopictus* combined with *Daphnia*. Values above the dashed line (0.5) indicate predator preference for mosquitoes and values below the dashed line indicate predator preference for *Daphnia*.

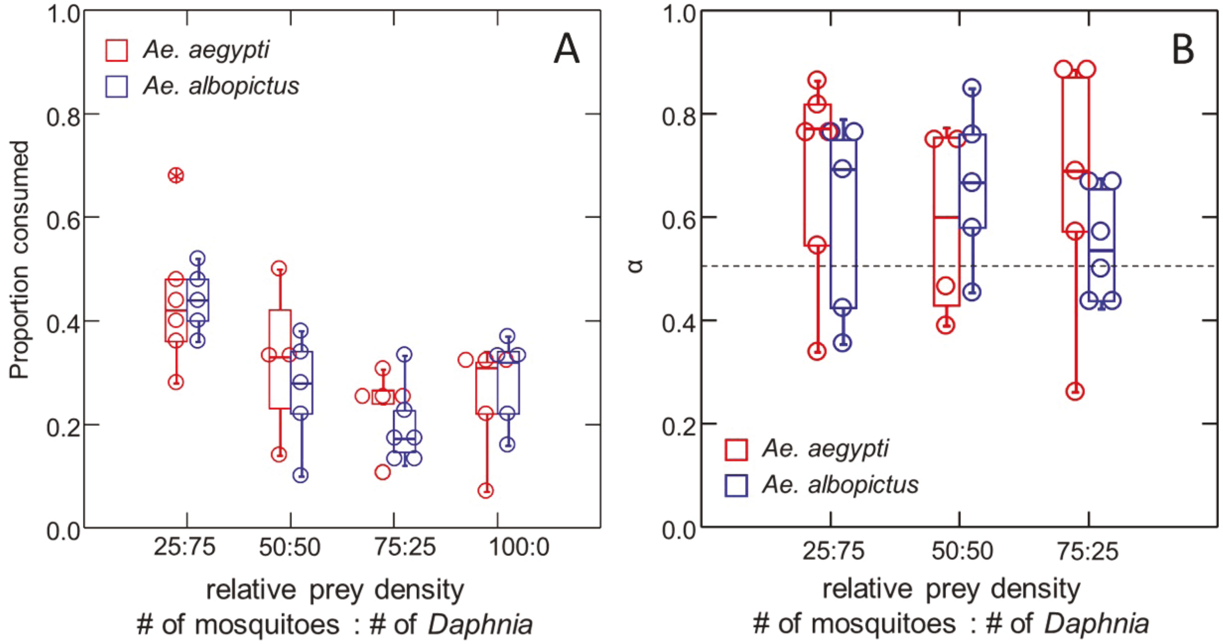

Figure 3. (A) Proportion of mosquitoes consumed and (B) Manly-Chesson α is plotted as a function of relative prey density (25:75, 50:50, 75:25) and larval mosquito species (*Ae. aegypti* or *Ae. albopictus*). The single prey control is also shown for both mosquito species in 3A (100:0).

Variation in individual behavior is common and results from several internal and external factors. Genetics, non-genetic factors such as environment, age, size, history of feeding, history of reproduction (Marten and Reid 2007), and genetic by environment interactions (Saltz et al. 2018), may play a role in this and other systems. Although common, this variation in predation rate, even among similar-sized individuals of the same species, highlights the difficulty in predicting the ultimate outcome of biological control strategies in any particular system.

The influence of alternative prey types on the feeding behavior of copepods not only depends on individual copepod behavior but also on the structure of the underlying community. Studies examining predation on larval mosquitoes in the absence of alternative prey options often find significant reduction in mosquito survival in the presence of a predator (Lounibos et al. 1993). However, the inclusion of non-mosquito prey often modifies rates of mosquito predation (Marten 1990a, Blaustein 1998, Lundkvist et al. 2003, Kumar and Rao 2003, Rey et al. 2004, Kumar et al. 2008, Cuthbert et al. 2019). The degree to which non-mosquito prey influences consumption is clearly dependent on the identity of individual predator and prey (Marten 1990a, Blaustein 1998, Lundkvist et al. 2003, Kumar and Rao 2003, Rey et al. 2004, Kumar et al. 2008, Cuthbert et al. 2019). Andreadis and Gere (1992) found that mosquitoes were not consumed by *A. vernalis* in the presence of *Euglena*. Alshammari et al. (2015) and Cuthbert et al. (2019) found reductions in consumption of *Aedes* larvae in the presence of *Paramecium sp*., though this reduction varied across copepod species.

The effects of cladocerans as alternative prey to larval mosquitoes are not consistent. The findings of our study are consistent with Kumar et al. (2008) who found no effect of cladoceran prey on consumption and selectivity of early instar mosquitoes regardless of density and across multiple predators (mosquitofish, dragonfly naiads, and the predatory copepod *Mesocyclops aspericornis*). However, a recent study by Cuthbert et al. (2020b) showed recently that the notonectid (*Anisops debilis*) preferred *Daphnia* over larval mosquitoes across a range of densities.

In addition to the individual and community-based factors which influence consumption and control of mosquitoes, there are a variety of extraneous developmental and abiotic factors which could also influence control outcomes in practice. First, *Acanthocyclops spp.* are primarily predaceous but have the potential to compete with mosquitoes as they consume microbes in earlier stages of development (Kumar and Rao 1998, 1999). This change in diet throughout development and typical cohort structure of *Acanthocyclops* likely restrict the window of predator-prey dynamics to certain time periods when adult copepods dominate the population. Second, predation by copepods has been shown to grow less effective as the mosquito ages and is likely not at all effective on later instars (Andreadis and Gere 1992, Udayanga et al. 2019). Thus, the window for copepods to efficiently prey on larval mosquitoes is several days. Third, both development time and predation rates are temperature-dependent; Calliari et al. (2003) found higher predation rates of multiple cyclopoid species at 26˚ C relative to 16˚ C. Finally, predators can also often change prey behavior, which may influence growth, survivorship, and sex ratios (Cardôso et al. 2013, Awasthi et al. 2015, Cuthbert et al. 2018). As a result, the strength of these interspecific interactions often varies temporally.

Our study demonstrates that *A. vernalis* could be effective in controlling mosquitoes in certain contexts. However, the utility of *A. vernalis* as a biological control agent in practice remains uncertain. Although on average we found a preference for *Aedes*, *Daphnia* was the preferred prey item for some copepods. This variation can contribute to uncertainty in the efficacy of biological control (Cuthbert et al. 2020a, 2020b). Studies have emphasized the utility of copepods in the genera *Mesocyclops and Macrocyclops* as biocontrol agents for multiple species of mosquito while rejecting the utility of *Acanthocyclops* (Marten 1989, 1990a, 1990b, Marten et al. 1994, 2000a, Schreiber et al. 1996, Rey et al. 2004, Cuthbert et al. 2018). Bolstering these claims are results that demonstrate that *A. vernalis* predators leave some mosquito larvae unconsumed when implemented as control agents (Marten 1990a, Alshammari et al. 2015). Paradoxically, predation may do more harm than good to mosquito populations. Incomplete consumption or removal of larval mosquitoes from a population can release surviving congeners from competition, thereby increasing the number of surviving individuals with those survivors being larger and having enhanced vector competence (Bevins 2008, Alto and Lounibos 2013, Alto et al. 2013, Neale and Juliano 2019). Furthermore, incomplete consumption has also been shown to have no discernible effect on adult mosquito populations in the long-term (Marten 1990a). Ultimately, integrative strategies of vector control are needed given the complex set of food webs in which larval mosquitoes are often embedded. Though *A. vernalis* does not seem like a worthy contender for biocontrol in comparison to *Mesocyclops* and *Macrocyclops spp.*, the implementation of *Acanthocyclops*, especially in systems that are abundant with this genus and systems in which mosquito larvae are not the only prey item, should be studied further. Further field tests solidify the role of copepod biocontrol.

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DATA ACCESSIBILITY STATEMENT

The data that support the findings of this study are openly available in Dryad Digital Repository: https://doi.org/10.5061/dryad.g79cnp5qq.

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