

Interactions Between Mosquito Larvae and Species that Share the Same Trophic Level

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Abstract

Ecological theory predicts, and empirical research shows, that species sharing the same trophic level as a target species (hereafter controphic species) can have large direct and indirect effects on the target species by sharing resources and/or by serving as alternative prey to predators. Yet, the roles of controphic species of mosquito larvae in affecting mosquito populations have received little attention. Published empirical evidence, although scarce, suggests that controphic species such as zooplankton and anuran larvae compete with mosquito larvae, can positively affect mosquito larvae by consuming bacteria that are pathogenic to mosquito larvae, reduce predation on mosquito larvae by serving as alternative prey, and ultimately cause increased predation on mosquito larvae by causing a numerical response in the predator. We conclude that more extensive theoretical and empirical studies in elucidating the roles of controphic species will better allow us to predict mosquito population dynamics and allow for better management of mosquitoes.

Controphic

species: two or more species sharing the same trophic level but not necessarily the same functional food groups

Apparent

competition: two or more prey species that share the same predator have a mutually negative interaction because they contribute to increased predator populations and thus to ultimately higher predation intensities on each prey species

Apparent

mutualism: two or more prey species sharing the same predator have reduced predation intensity because the predator can feed on these alternative prey

INTRODUCTION

Ecologists strive to understand how various factors, including abiotic conditions and interspecific interactions, contribute to distribution and abundance of a particular species of interest (hereafter called target species). Decades of modeling, observational studies and experimental approaches have led ecologists to conclude that species sharing the same trophic level (hereafter called controphic species) often play important but highly diverse roles in affecting each other (22, 26, 32, 33, 40, 86). Traditionally, interactions among controphic species were viewed as a simple, mutually negative interaction either directly through interference or indirectly through exploitation of shared resources (**Figure 1**). Understanding such mutually negative interactions among competing species remains a cornerstone of community ecology (48).

More recently, community ecologists have recognized the way in which controphic species can indirectly interact with one another when embedded in complex communities. We list examples of the modules (37) by which controphic species interact indirectly with one another in addition to the interspecific competitive interactions discussed above (**Figure 1**).

Apparent competition (36) occurs when two (or more) prey species share a common predator, and the predator's numbers are limited by prey availability. By presenting itself as an additional food resource, the second prey species allows the abundance of the predator to increase and, as a result, reduces the density of the target species. A similar mechanism is the case of competition for enemy-free space (44), in which prey species are confined to using certain resources (e.g., refuges, food types) in the presence of predators. If more than one prey species is present, and both utilize those enemy-free resources, the species can limit each others' numbers.

An apparent mutualism between prey species that share a common predator can arise if predator populations are limited by

factors other than prey availability (as is the case for apparent competition) (1, 3). In this case, the presence of a controphic prey species satiates the predator, thus allowing a relief of predation pressure on the target species; that is, the controphic species indirectly benefits the target species.

When the enemy of the target species is a parasite or pathogen, a mechanism similar to apparent competition arises if the controphic species, which are also hosts to the parasite, are equally susceptible to that pathogen/parasite (38). In this case, the presence of the second controphic species can cause the target species to have a higher infection prevalence. Alternatively, a mechanism similar to apparent mutualism occurs if one of the controphic species is a poor host for the pathogen/parasite, and the presence of the controphic species can allow the target species to have a lower infection prevalence (38).

If controphic species and target species consume resources in different functional groups, and the resources themselves compete for their own limiting resources, their presence can provide an indirect mutualism on the target species (94). For example, in aquatic ecosystems, controphic herbivore species include species that consume periphytic algae that grow on substrate (e.g., snails and tadpoles) and species that consume phytoplanktonic algae suspended in the water (e.g., zooplankton). By reducing the abundance of one group of algae and releasing nutrients (through excrement), the presence of one controphic species can enhance the rate of production of the other group of algae and indirectly facilitate the controphic species (58).

The controphic species can also be an intraguild predator (i.e., eats the target species) or an intraguild prey (i.e., is eaten by the target species) in addition to sharing common resources (41). In this case, the net impact of the controphic species on the target species depends on whether it is an intraguild predator or intraguild prey, as well as whether it is a superior or inferior competitor for the shared resource (41).

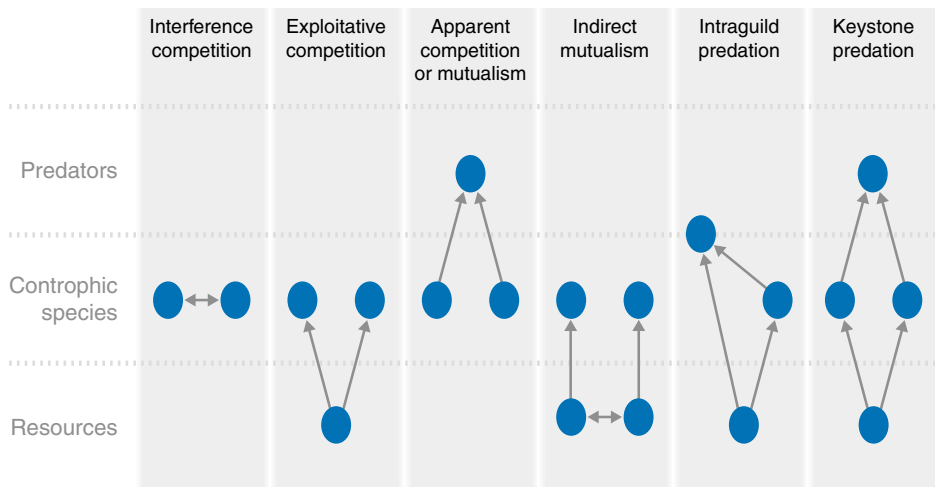


Figure 1

Schematic diagrams of the modules by which species can both directly and indirectly affect a target species (modified from Reference 37). Here, we focus specifically on controphic species and the way that they interact with each other, resources, and predators. One-way arrows point to the consumer. Two-way arrows designate a mutually nonconsumptive negative interaction.

The controphic species can share both predators and resources. Here, the impact of the controphic species on the target species depends on a balance between competition for resources and apparent competition through shared predators (39, 57). The presence of a controphic species and predator can benefit the target species if the former is more susceptible to predation, but harm the target species if the former is less susceptible to predation.

The above six mechanisms (also see **Figure 1**), as well as many other more specific cases, illustrate the rich diversity of effects, other than interspecific competition, that controphic species can have on one another when they are embedded in a complex food web. The question of how controphic species affect a target species enters the realm of applied ecology when the target species in question is considered a nuisance or pest (30, 46) or a rare endangered species (79).

Numerous studies document that species sharing the same trophic level of agricultural pest species indirectly affect pests via shared predators, parasitoids, and/or parasites (re-

viewed in Reference 96). In fact, traditional ideas of preferable traits for natural or introduced biological control agents in agricultural systems included generalist predators whose population sizes would increase when the pest species was not abundant by feeding on alternative prey (28, 84).

Surprisingly, the role of controphic species as an important component affecting another important group of pests, mosquitoes (Diptera: Culicidae), remains largely unexplored, even though controphic species of mosquitoes likely have a strong impact on mosquito populations and may more likely be an effective management tool for controlling mosquito populations than for controlling agricultural pests for at least two reasons. First, controphic species of agricultural pests are generally pests themselves (or at best, weaker pests; 34, 47), whereas a wide array of controphic species of mosquito larvae are not pests. Second, controphic species of mosquito larvae are often orders of magnitude more abundant than mosquito larvae (7, 11), and thus they should have a greater effect via competition and mediating predator effects.

Traditionally, scientists with backgrounds in medicine, and not community ecology, studied mosquito biology (89), and they understood that controlling mosquito populations was necessary for human health (particularly in tropical regions). As a result, even though conceptual community ecology has been used in various applied fields for decades (e.g., biological control) (28, 75), the application of basic community ecological principles to mosquito ecology and control has lagged. However, the basic principles of community ecology should apply to mosquitoes, particularly to their larval habitats, where interactions with resources, predators, pathogens, and controphic species can be important (73, 74).

Mosquito larvae develop in lentic habitats ranging in size from small, water-filled axils of plants to vast wetlands, and from highly ephemeral to permanent. Because small, lentic habitats are convenient systems for testing ecological theory (19, 27, 50, 99), considerable information is known generally about how different components of these systems affect populations and community structure. This knowledge can be applied to predicting how controphic species might affect mosquitoes under varying conditions and how controphic species might be manipulated to reduce the success of mosquitoes. We restrict this review to mosquito-nonmosquito interactions. Mosquito-mosquito interspecific interactions, a fairly well-studied topic in container habitats, have been recently reviewed (45, 60). Furthermore, except for when we consider oviposition habitat selection, we focus almost entirely on the larval stage and how interactions within that stage influence populations. An important limitation of mosquito ecology to date is the lack of knowledge of interactions and influences on the adult stages of mosquitoes, which future studies should incorporate.

As discussed above for the general case, controphic species may ultimately affect mosquitoes in a variety of direct and indirect ways (**Figure 1**). Below, we discuss each of

these in general and examine the available evidence in the mosquito ecology literature.

Interference and Exploitation Competition

Interference competition (a direct physical or chemical negative interaction) and exploitative competition (indirect negative interaction by depletion of resources) are important forces affecting abundance and distribution of herbivorous and detritivorous species in lentic habitats (99). It has been argued that the role of competition in ephemeral aquatic habitats is a function of hydroperiod length (reviewed in Reference 98). This scenario suggests that competition (particularly exploitative competition) is less likely to be important in habitats of short hydroperiod or in the early periods of longer-lived ephemeral habitats because densities of competitors are unlikely to be high and resources are unlikely to be reduced. Competition should increase during the middle period of long-lived habitats because densities of competitors are likely to be much higher at the end period of moderate hydroperiod habitats. Moreover, risk of desiccation should not supplant the importance of competition but exacerbate it, because competition works to increase the time it takes for an individual to reach metamorphosis and emerge from the aquatic habitat into adulthood (4a), enhancing the risk of desiccation from habitat drying.

Depending on the species, mosquito larvae may filter feed particulate matter such as phytoplankton, microorganisms, and detritus; they may graze on periphyton; or, in fewer cases, they themselves may be facultative or obligate predators. Densities of species controphic to mosquito larvae often reach high densities and deplete resources, including periphyton grazers such as snails and tadpoles (20, 21, 100) and phytoplanktivorous cladocerans (58, 91). Some of these controphic species also use interference (5, 68). Thus one might expect a priori that interspecific competition with controphic species would be

Table 1 Experimental evidence for competitive interactions between mosquito larvae and controphic species

Larval mosquito–controphic species	Venue	Effect of controphic species	Reference(s)
<i>Culiseta longiareolata</i> larvae– <i>Bufo viridis</i> tadpoles	Outdoor artificial pool experiment	<i>Bufo</i> tadpoles preyed upon <i>Culiseta</i> , reduced size at metamorphosis, increased time to metamorphosis.	17, 18
<i>Culex quinquefasciatus</i> – <i>Limnodynastes peronii</i> tadpoles	Lab experiment	Tadpoles reduced development and survival rates, even at high food levels. Fungicides reduced or eliminated effect.	67–70
<i>Ochlerotatus australis</i> – <i>Crinia signifera</i> tadpoles	Lab and outdoor artificial pool experiments	Tadpoles reduced development and survival rates, even at high food levels. Fungicides reduced or eliminated effect and increasing densities increased effects.	67–70
<i>Anopheles quadrimaculatus</i> –zooplankton	Outdoor artificial pool experiment	Zooplankton reduced survival and increased time to metamorphosis.	53
<i>Culex pipiens</i> – <i>Daphnia</i> / <i>Heterocypris</i> (Crustaceans)	Outdoor artificial pool experiment	Crustaceans reduced survival to and size at pupation.	90
<i>Wyeomyia</i> -cladocerans	Lab experiment	Cladocerans did not affect growth or survival.	66
<i>Culex tarsalis</i> -zooplankton ^a	Enclosures in outdoor rice plots	Mosquitoes developed quicker in the presence of mosquitofish (which decreases zooplankton).	14
<i>Daphnia</i> –mosquito–edible/nonedible algae ^a		Shows that some algae at high concentrations are toxic or inedible to mosquitoes. Suggests that <i>Daphnia</i> will reduce edible algae and increase nonedible.	65

^aThe last two studies provide evidence that competition exists, but they are not direct experimental assessments of the competition question.

important in affecting mosquito survival and development in habitats that exceed the minimum hydroperiod needed to complete metamorphosis, when resources are limiting, and in habitats that do not experience high predation intensity (see below).

Table 1 shows the paucity of experiments that have explicitly tested for competitive effects between mosquito larvae and non-mosquito controphic species. The interaction that has received the most attention is that between mosquito larvae and anuran tadpoles; all three mosquito-tadpole systems tested have displayed strong interphyletic competition (17, 18, 67–70). However, the mechanism of interspecific competition appears to differ between two of the systems. In Australia, in both freshwater and brackish water systems, competition appeared in large part to be through an interference mechanism because the strength of competitive interactions was not weakened when high levels of

food were added (69). However, in Israeli desert rock pools, the strong competitive effects between mosquitoes (*Culiseta longiareolata*) and tadpoles (*Bufo viridis*) (17, 18) essentially disappeared when high levels of food were added (L. Blaustein & B.P. Kotler, unpublished data). Other experimental assessments show competitive effects by controphic zooplankton assemblages on *Anopheles quadrimaculatus* (53), *Culex pipiens* (90), and *C. longiareolata* (90). The mode of competition by these zooplankton assemblages has not been explored. We are aware of only one published study that failed to detect evidence for interspecific competition between mosquitoes and controphic species—cladocerans potentially sharing resources with the mosquito *Wyeomyia smithii* in the water-filled leaves of pitcher plants (66).

We must conclude that although the bulk of the evidence accumulated thus far supports a role for strong interspecific competition by

Intraguild

predation: case in which two or more potential competitors prey upon each other

BTI: *Bacillus thuringiensis* var. *israelensis*

controphic species on mosquito larvae, the evidence remains preliminary. First, in most cases, experiments take place in mesocosms where nutrient conditions (and other factors) may be different from that of natural pools. Second, experiments that yield negative results are less likely to be published. Third, there is a general paucity of studies. More studies on the simple impact of competitors on mosquito larvae are necessary to gain a more general understanding of this mechanism's importance to mosquito populations.

Apparent Competition and Apparent Mutualism with Shared Predators

Strict apparent competition and apparent mutualism scenarios require that the target and controphic species share predators but not food (Figure 1). Although we are unaware of any studies on mosquitoes and their controphic species that show strict apparent competitive or mutualistic scenarios, because they likely also share food, there are some possible cases in which such indirect effects might exist. For example, mobile generalist predators, such as fish, may forage in different habitat types, such that a controphic species from one habitat type could influence the density of fish in another habitat type by serving as prey (85) and, as a result, influence the predation rate on mosquitoes in the second habitat. If the mobile generalist predator increases its density, this could result in an apparent competition scenario, whereas if the mobile generalist predator species spends more time consuming the controphic species, this could result in an apparent mutualism scenario.

Intraguild Predation

Mosquitoes and controphic species may also be intraguild predators. In rock pools in the Negev Desert (Israel), in addition to consuming the same resources and competing with one another, *C. longiareolata* larvae and toad (*B. viridis*) tadpoles mutually prey upon each other; which species is predator and which

is prey depends primarily on the relative size of the individuals (17, 18). Individual size, in turn, is determined primarily by which species colonizes the pool first. Thus, the presence of the controphic species (toad tadpoles in this case) can either benefit or inhibit the mosquito species.

Some mosquito larvae such as *A. quadrimaculatus* may prey upon the early stages of cladocerans (96a). Mosquito larvae commonly prey on protozoans, often having a large impact (4, 51, 52), but can also compete with them for bacterial resources (25, 52). Thus, it is possible that protozoans could either benefit or harm mosquito populations, depending on the balance between their effects as intraguild prey and as competitors. *Aedes sierrensis*, a tree hole mosquito, and the protozoan *Lambornella clarki* represent a unique intraguild predation/parasitism relationship (97a). The mosquito preys on the free-living ciliate. However, the presence of the mosquito induces the transformation of the protozoa into an obligate parasite of the mosquito.

A complex scenario that is not strict intraguild predation, but shares some similarities, is when entomopathic bacteria such as *Bacillus thuringiensis* var. *israelensis* (BTI) are applied for mosquito control (19a). Mosquito larvae are killed when they feed on sufficient BTI spores. BTI does not replicate inside the gut of the mosquito larva, but the spore contains protein crystals that are toxic to the mosquito larvae. BTI spores do not stay in suspension for long periods, but they quickly adsorb to the sediment. Consequently, although the spores are still potentially pathogenic to mosquito larvae if consumed, filter-feeding mosquito larvae no longer can efficiently consume the spores adhering to the substrate. However, some protozoa, such as *Tetrahymena*, feed in both the sediment and water column. Laboratory studies suggest that the *Tetrahymena* consume the BTI cells in the sediment and accumulate the toxic protein crystals. They themselves are unaffected by the BTI protein crystals. The *Tetrahymena* then can deliver the BTI when they enter the water

column and are ingested by the mosquito larvae (63, 64). How effective such protozoans may be in increasing efficacy of BTI under field conditions remains to be tested.

Another similar but more complicated scenario is the case in which controphic species indirectly influence mosquitoes by consuming possibly harmful bacterial pathogens such as BTI. Whereas BTI is toxic to mosquito larvae when consumed, most other controphic species, such as crustaceans, that ingest the bacteria do not incur mortality (77, 83, 92). It is then possible that those controphic species that are not intraguild prey of the mosquito larvae, through their consumption, reduce the amount of the pathogenic bacteria available for consumption by mosquito larvae. In this case, the net effect of the controphic species on mosquitoes depends on the balance between the positive respite they receive from the pathogenic bacteria and the negative impact of the controphic species on the mosquito's other food resources. We suspect that the net effect is most likely positive, as BTI applications are meant to cause up to 100% mortality of mosquito larvae. Few studies have addressed this problem, although those that have suggest that zooplankton may play a significant role in affecting the efficacy of pathogenic bacteria to kill mosquitoes (6, 16, 93).

Indirect Mutualism

Indirect mutualisms arise when controphic species benefit each other by consuming different parts of the resource base, which themselves compete for limiting resources. For example, in pond ecosystems, periphyton and phytoplankton compete for nutrients, and blooms of phytoplankton can reduce UV radiation necessary for periphyton photosynthesis (35). An herbivore that consumes one group of algae (periphyton or phytoplankton) is likely to confer an advantage to the second group of algae both by reducing the competitive ability of the algae and by recycling nutrients. Thus,

we might expect efficient periphyton grazers such as tadpoles and snails to indirectly positively affect filter-feeding mosquitoes such as most *Anopheles* and *Culex* species. Likewise, we might expect that efficient phytoplankton filter-feeders such as *Daphnia* would positively affect mosquito larvae that are primarily periphyton grazers such as some *Aedes* and *Culiseta*. As far as we know, there are as yet no clear tests of this for mosquitoes and their controphic species.

Stav et al. (90) provide some indirect tests of this mechanism and demonstrate that a zooplankton assemblage (primarily filter-feeding *Daphnia* with fewer grazing *Heterocypris*) caused a decrease in phytoplankton and an increase in periphyton. As expected, phytoplankton filter-feeding *C. pipiens* did worse in the presence of these controphic species. We might expect that *C. longiareolata*, thought to be primarily a periphyton grazer (95), might do better in the presence of this zooplankton assemblage than in its absence; this was not the case, and instead, there was a small reduction in survival (90). However, although *Culiseta* is primarily a grazer, it can also filter-feed on phytoplankton (95). Moreover, increases in periphyton may not necessarily translate into increases of highly edible periphyton.

This indirect mutualism outlined above, although an interesting indirect effect that could arise between controphic species, may not be commonly important for mosquitoes in nature. This is because many mosquito species both graze and filter-feed, and many natural controphic species assemblages have both filter-feeders and grazers. One example of an exception may be rock pools in intermittent river beds of the Negev Desert. Here, filter-feeding zooplankton are not common, and grazing anuran tadpoles can be abundant. High densities of *B. viridis* tadpoles strongly depress the periphyton-grazing *Culiseta* larvae (17, 18), whereas filter-feeding mosquitoes such as *Culex* and *Anopheles* may instead benefit from the presence of controphic toad tadpoles. The latter scenario has yet to be tested.

Keystone

predation: inferior competitors increase in abundance owing to reduced abundance of a superior competitor caused by a predator

Competition for Resources and Shared Predators

This more complex module includes four players, the mosquito and the controphic species, both of which share common resources and common predators (**Figure 1**). If the predator's negative effect on mosquito larvae is outweighed by its reducing competition by controphic species, then the predator can be thought of as a keystone predator (57, 81), allowing mosquitoes with controphic species to do better in the presence of predators. Conversely, if the controphic species serve as alternative prey as well as potential competitors and thus reduce the negative effect of predation on mosquito larvae, then the net effect of the controphic species on mosquito larvae is positive and is akin to the apparent mutualist scenario discussed above.

We are aware of a few studies that have assessed the interaction between predation and competition among mosquitoes and their controphic species. Blaustein & Karban (14) performed a study comparing the development rates of *Culex tarsalis* mosquito larvae in predator-free cages placed within flooded rice plots that either did or did not have predatory mosquitofish (*Gambusia affinis*). They found that mosquitofish actually benefited the mosquito larvae: In the presence of mosquitofish, the mosquito larvae developed faster and more survived to pupation, most likely because mosquitofish drastically reduced filter-feeding zooplankton densities, which in turn were likely strong larval mosquito competitors (14). Bence (7) performed a similar study on the interaction between mosquitofish, zooplankton, and *C. tarsalis* and found similar but not statistically significant results. However, in both studies, mosquitofish had an overall negative effect on *C. tarsalis* densities outside the predator-free enclosures (7, 9), and thus neither result is consistent with the traditional keystone predation mechanism. When exposed to mosquitofish and not caged, the negative

consumptive effect on the mosquito larvae still outweighs the positive effect of reduced competition.

No keystone predator effect was observed for the survival or growth rates of *A. quadrimaculatus* larvae in experimental mesocosms with zooplankton competitors and predatory backswimmers (*Notonecta undulata*) (53). This result occurred presumably because the overall net effect of predators on mosquitoes was so strong that the concurrent reduction of controphic zooplankton could not provide a respite from this intense predation. Finally, Stav et al. (90) found that both competitors (a zooplankton assemblage) and predators (larvae of the dragonfly *Anax imperator*), when alone, reduced the success of *C. pipiens*, whereas when both predator and competing controphic species were together, there was neither net advantage nor disadvantage conferred to the mosquito. In this case, the predator did not reduce zooplankton densities, and thus it appears as if the negative effect of competition and the positive effect of reduced predation intensity afforded by the alternative prey cancelled each other out.

Marten's (65) suggestion of how controphic species may influence mosquito larvae is a slightly more complex version of the keystone predator module (**Figure 1**). He proposed not only that cladocerans reduce the concentration of algae that are edible to the mosquito larvae, but also that the competitive release between algal species caused an increase in inedible green algae, a commonly reported phenomenon in aquatic systems (31, 56). To our knowledge, this mechanism has not been pursued further with regard to mosquito larvae. Below, we describe scenarios that have this basic food web structure, but with added complexities to various interactions that have been observed in controphic-mosquito interactions when there are shared resources and predators (see Reference 22 for a more general review of these scenarios).

No Numerical Response of Predators

Just like in the apparent competition scenario described above, the strict keystone predation mechanism requires a strong and immediate numerical response of predators to prey populations and also assumes equilibrium dynamics; otherwise, the expected outcomes become more complex (2, 78). In mosquito-controphic species food webs, there are many cases in which numerical responses of predators are not expected, at least in the short-term, and the system is nonequilibrium.

One often observed scenario is that the presence of the controphic species, at least initially, results in lower predation pressure on the mosquito larvae. In some cases, this may be due to turbidity caused by benthic controphic species such as fairy shrimp and clam shrimp stirring up the sediment as they forage at the bottom of the water body (62). This turbidity could reduce the predator's efficiency to detect and catch mosquito larvae and other prey, as has been demonstrated with predatory fishes (8). A more likely common mechanism is that the controphic species serve as an alternative prey source for the predator, thus diluting predation intensity on mosquito larvae in the absence of numerical predator responses. This has been demonstrated in a number of laboratory and outdoor enclosure experiments (7, 10, 13, 24, 59).

How much the alternative prey reduces predation on mosquitoes depends on the predator's preference for the different prey, the controphic species/mosquito larvae abundance ratios, and the interaction between the two. Preference (or selectivity) for mosquito larvae relative to controphic prey depends on many factors, including:

- The species of mosquito. For example, given equal numbers of different prey items in a cafeteria experiment, *Notonecta maculata* preys at a much higher rate on the mosquito *C. longiareolata* than it does on *Daphnia magna*, but the relative difference in predation rates be-

tween *Culex laticinctus* and *D. magna* is smaller (12).

- The species of predator. For example, some species of diving beetles (Dytiscidae) prefer *D. magna* species to *Culex* larvae, whereas other congeneric species strongly prefer the opposite (61). The dragonfly larvae *Pantala hymenaea* prefers *Culex* larvae to *Chironomus plumosus* midge larvae (82), while *Notonecta maculata* preys far more heavily on *C. laticinctus* larvae than on *Chironomus* larvae (12).
- The relative sizes of the predator, mosquito, and alternative prey. For example, cyclopoid copepods are small compared with most other mosquito predators and are generally ineffective at preying on larger instars. When the predatory cyclopoid copepod *Mesocyclops thermocycloides* was offered equal numbers of first-instar mosquito larvae (*Anopheles stephensi* or *Culex quinquefasciatus*) and medium-sized cladocerans (*Ceriodaphnia cornuta* or *Moina macrocopa*), they strongly preyed more heavily on the mosquito larvae (54). However, when offered fourth-instar mosquito larvae, which are too large for *M. thermocycloides* to capture, and medium-sized cladocerans, the predators preyed more heavily on the cladocerans (54).

The abundance of mosquito larvae relative to the abundance of controphic species varies greatly among habitat types. In container habitats such as phytotelmata (50) or other relatively small habitats such as flashflood-prone rock pools (97), mosquito larvae are often one of the most abundant prey species available to a generalist predator. Alternatively, in larger habitats, such as flooded rice fields and wetlands, mosquito larvae are typically rare prey relative to controphic species such as zooplankton (7, 11, 23). If predation rates on mosquito larvae are proportional to the ratio of available prey species (24), investigators may predict that, in the

Numerical response: changes in predator densities in response to changes in prey densities, from conversion of prey energy into either reproduction or immigration

Developmental response: the growth of individual predators in response to prey consumption

absence of predator numerical responses, the reduced predation on mosquitoes caused by controphic species may be considerably less in small-container habitats than in large wetlands. Moreover, predators may switch and eat disproportionately more of the abundant prey types and disproportionately less of the rare prey types (72, 76). This frequency-dependent predation, which is common in arthropod predator-prey systems (reviewed in Reference 87), would reduce further the effect of alternative prey on predation on mosquito larvae in small-container habitats and increase the effect in larger habitats such as wetlands.

Predator Numerical Responses

In habitats where predators show strong developmental (i.e., growth) and or numerical (i.e., reproduction and/or recruitment to a particular habitat) responses to prey availability, particularly those with longer hydroperiods (98), the interaction between controphic species and larval mosquitoes depends on a balance between the species' competition for shared resources and their apparent competition for shared predators (39, 57). Numerical responses to prey availability are frequently expected but rarely measured experimentally in aquatic ecosystems (but see Reference 20); to our knowledge, no studies have specifically measured predator numerical response to mosquitoes and their controphic species.

In the simplest keystone predator module (**Figure 1**), whether mosquito larvae are benefited or harmed by the presence of the controphic species depends on which species is a better competitor for resources and which is more susceptible to predators (i.e., a worse apparent competitor). A trade-off between these abilities is necessary for the species to coexist (39, 57). If mosquito larvae are superior resource competitors and more susceptible to predators, the addition of a controphic species reduces mosquito abundances, whereas if mosquito larvae are weaker resource competitors but less susceptible to pre-

ation, the presence of a controphic species benefits mosquito larvae abundances.

The role of hydroperiod length in mosquito interactions in food webs.

Predators may colonize a pool (e.g., predatory insects and salamander larvae), they may arise from drought-resistant resting stages (e.g., cyclopoid copepods and turbellarian flatworms), or they may be introduced as biological control agents of mosquitoes (e.g., mosquitofish and other larvivorous fishes). Regardless of how they become part of the community, overall predation intensity on their prey should increase with the length of the hydroperiod (98). When a mosquito and a controphic species share the same predator, the overall effect of the controphic species may thus vary considerably along a hydroperiod gradient, both within a habitat, as the length of time it holds water increases, and among habitats that vary in their hydroperiod length.

In short-hydroperiod wetlands, upon initial inundation, interspecific competitors such as zooplankton hatch from resting eggs and can become dense. By competing with mosquito larvae, these interspecific competitors may reduce the density of larval mosquitoes, in addition to increasing their development time, which puts them at risk of desiccation when the habitat dries (23, 31a, 53). Furthermore, for mosquitoes that exhibit developmental plasticity in response to desiccation (46), competitors can also reduce size at metamorphosis of mosquitoes. Most studies show that individuals that metamorphose at a smaller size have reduced fitness (80). In intermediate hydroperiod habitats, or those that dry intermittently (23), predation intensity increases, but so does predation on controphic species. This may benefit mosquito larvae if predators reduce the impact of competitors, but the predators themselves do not have numerical responses to control mosquito numbers. Finally, in longer-hydroperiod habitats, predators can become dense and exhibit numerical responses to both mosquitoes and

controphic species, reducing all of their numbers considerably (23).

Effect of productivity on mosquito interactions in food webs. From theoretical arguments (22, 39, 57), the impact of predators on mosquitoes and controphic species may be expected to vary along a gradient of primary productivity (e.g., nutrient inputs). In a simple keystone predator module, in which competitive ability and predator vulnerability are inversely related, increasing productivity will change the outcomes of competitive interactions among the controphic species. If the larval mosquito is the superior competitor, but is more susceptible to predators, controphic species will be outcompeted at low productivity, can coexist and negatively impact mosquitoes at intermediate productivity, and eliminate mosquitoes through apparent competition at high productivity. Alternatively, if mosquitoes are inferior competitors but less susceptible to predators, the opposite results are expected along a productivity gradient. This scenario would be predicted provided that predators show a strong numerical response to variation in productivity. Moreover, the predicted outcomes of these interactions along the productivity gradient assume a positive linkage between mosquito survival/emergence in a given water body and oviposition rates. Although such effects have not been examined in mosquito–controphic species systems, they have been observed in other parts of the aquatic food web (20, 21, 91).

Role of Oviposition Habitat Selection

Much of what we have considered thus far has been the effect, or predicted effect, of controphic species at the level of a single pool. However, a mosquito population is not confined to a single pool. Instead, a mosquito population exists in the adult stage over a wider terrestrial area and includes a number of larval patches (i.e., water bodies). There are increasing numbers of studies that show that mosquito females consider controphic

densities or larval food resource levels when ovipositing (15, 49, 70, 71). Thus, by choosing the best-quality sites (here, low conspecific densities), oviposition habitat selection in response to conspecific densities should mitigate regionally the overall effect of controphic species. This needs to be considered with all other factors that might influence oviposition habitat selection such as risk of predation (88). Further study may show that the oviposition response to controphic densities may not be linear, as observed in a study of oviposition response to conspecific density (29), or that high food resource levels supersede high conspecific densities. Mosquitoes may prefer to oviposit where controphic densities are present if food resource levels are adequate to reduce predation intensity on mosquito larvae.

Example: The Case of Mosquitofish Introduced into Rice Fields for Mosquito Control

We have argued that early in a long-lived temporary water body, where predator numerical effects are not important, controphic species should have an indirect net mutualistic effect on mosquitoes, whereas when predator numerical effects are important later in the season, controphic species should have an indirect net negative effect on mosquitoes through apparent competition. In fact, this sort of scenario has been proposed to explain results observed in flooded rice fields in the Central Valley of California (43). Rice fields are generally flooded in spring for about four months, after which the fields are drained so that the rice can be harvested. Various mosquito species can be found across the flooded season, although *C. tarsalis* (the primary vector of Western equine encephalitis and West Nile virus) is generally most abundant in the beginning of the season and *Anopheles freeborni* (a potential malaria vector) is most abundant toward the end of the season (42, 43). Rice fields have complex food webs (55), and although the mosquitoes emanating from these rice fields are of great nuisance

and medical concern to humans, they probably have rather negligible influences in the rice field community in that they are exceptionally rare compared with their controphic zooplankton (7, 11).

Mosquitofish (*G. affinis*) are commonly introduced into many of these rice fields for mosquito control. However, when one considers published experimental assessments of the effectiveness of mosquitofish on mosquito control, mosquito control ranges from nearly 100% control (7, 42) to actually increasing mosquito numbers, particularly early in the rice season (11, 43). Moreover, if one considers percent control as a function of stocking rate, there is no strong correlation. For example, Hoy et al. (43) suggested that a stocking rate of 100 mosquitofish per acre early in the season could result in negative control (higher mosquito densities with than without mosquitofish) but that 300 mosquitofish per acre should sufficiently control mosquitoes. In an experimental study in California rice fields, Blaustein (11) stocked nearly 1000 mosquitofish per acre and the mosquitofish population increased more than 60-fold by season's end. Yet, mosquitofish did not have a negative impact on mosquitoes. Why is the effect of mosquitofish so different among experiments if stocking rate and mosquitofish population growth rate are not the answer?

The efficacy of mosquitofish to control mosquitoes likely varies because of different environmental conditions, such as vegetation type and density, as well as different secondary productivities of controphic species. Mosquitofish have no distinct pref-

erence for mosquitoes over other controphic species (59). Mosquitofish may be effective in rice fields of low secondary productivities and ineffective at high secondary productivities (9). In fields with high controphic species presence, by the time mosquitofish have sufficiently reduced alternative prey to increase predation intensity on mosquitoes, the season might be over. That is, in ecological terms, there may be an interaction between top-down effects and bottom-up effects. Experimental manipulations of both top-down and bottom-up effects on rice field mosquitoes are needed to test this.

CONCLUSIONS

Because so much is known about mosquito biology, and because mosquito larvae are often embedded in comparatively simple food webs, found in habitats with well-defined boundaries, and easily replicable for ecological experimentation, larval mosquitoes and their interactions within a food web provide an excellent model system for testing and developing ecological theory (19, 27, 50, 99). Likewise, basic ecological principles apply to mosquitoes, and thus ecological principles should be used to better understand mosquito population regulation and control. We have outlined how controphic species, in the context of food webs, should affect mosquitoes. Relative to the potential importance of controphic species, which ecological theory suggests and the limited empirical information supports, we believe that considerably more research should be invested in this area.

SUMMARY POINTS

1. The role of controphic species on mosquitoes, by sharing resources and/or predators, has been largely neglected, although ecological theory suggests this component of the food web should be important in affecting mosquito populations.
2. Available empirical evidence indicates that controphic species such as zooplankton and tadpoles strongly and negatively affect mosquito larvae through competition.
3. Controphic species may lessen the efficacy of pathogenic bacteria applied for mosquito control by consuming these bacteria.

4. Laboratory and field studies indicate that, at least over a short-term, controphic species act as mutualists; by serving as alternative prey, they reduce predation intensity on mosquitoes.
5. Evidence in temporary water bodies indicates that owing to numerical responses of predators such as mosquitofish, the role of controphic species may switch from having a net positive effect on mosquitoes early in the season (reducing mosquito consumption by acting as alternative prey) to having a negative, apparent competitive effect late in the season by contributing to the increase in predator numbers.
6. Because controphic species may compete with mosquito larvae (larval periods are longer) and may alter oviposition habitat selection by mosquitoes, simply comparing the number of larvae in different treatments arising from wild female oviposition will not give an accurate picture of the effects of controphic species.

FUTURE ISSUES

1. Traditional experimental methods, and using mosquito density as a response variable, may have limited inference for the actual impact of controphic species on mosquito larvae. This is because strongly competing mosquito larvae often grow more slowly (53, 90), and thus habitats with stronger competitive impacts of controphic species may have the same or even higher densities of mosquito larvae simply because the development of those larvae is delayed. Moreover, mosquitoes emerging from habitats with controphic species may also be smaller, which often translates into lower fitness (80).
2. Oviposition may not be random with respect to controphic species, and there is increasing evidence that many mosquitoes avoid ovipositing where controphic species densities are high, larval food resources are low, or both (15, 70, 71). Understanding the importance of these behavioral decisions will play an increasingly important role in understanding the interactions between controphic species and mosquito larvae.
3. Can controphic species be managed to increase their effectiveness of mosquito control? Anthropogenic activities often result in short-hydroperiod habitats, which often have high densities of mosquito larvae. Management that increases the hydroperiod of habitats from short to intermediate (perhaps digging them deeper) will likely reduce mosquito emergence by increasing the negative effect of controphic species and predators (23).
4. In seasonal wetlands such as rice fields, it is often assumed that the impacts of introduced mosquitofish may change seasonally from apparent mutualism through their interactions with high densities of zooplankton to high predation rates on mosquitoes as a result of mosquitofish reproduction (11, 43). However, assuming this is the case, both modeling and empirical tests are needed to evaluate the interactive roles of initial mosquitofish: Controphic density ratios, secondary productivity, and oviposition habitat selection should be considered when determining the nature and intensity of mosquitofish effectiveness as a biological control agent in this type of habitat. The ability to predict secondary production (i.e., zooplankton in particular) may also allow us to predict better the efficacy of pathogenic bacteria such as BTI.

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Errata

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