

Review Article

Larvicidal Efficiency of Aquatic Predators: A Perspective for Mosquito Biocontrol

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(Accepted November 2, 2005)

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ABSTRACT

Ram Kumar and Jiang-Shiou Hwang (2006) Larvicidal efficiency of aquatic predators: a perspective for mosquito biocontrol. *Zoological Studies* 45(4): 447-466. Biological control of mosquito larvae with predators and other biocontrol agents would be a more-effective and eco-friendly approach, avoiding the use of synthetic chemicals and concomitant damage to the environment. Manipulating or introducing an auto-reproducing predator into the ecosystem may provide sustained biological control of pest populations. The selection of a biological control agent should be based on its self-replicating capacity, preference for the target pest population in the presence of alternate natural prey, adaptability to the introduced environment, and overall interaction with indigenous organisms. In order to achieve an acceptable range of control, a sound knowledge of various attributes of interactions between a pest population and the predator to be introduced is desirable. Herein, we qualitatively review a wide range of literature sources discussing the ability of different aquatic predators to control mosquito larval populations in environments where mosquitoes naturally breed. Different predators of mosquito larvae include amphibian tadpoles, fish, dragonfly larvae, aquatic bugs, mites, malacostracans, anostracans, cyclopoid copepods, and helminths. The most widely used biocontrol agents of mosquito populations are the western mosquito fish, *Gambusia affinis*, and the eastern mosquito fish, *G. holbrooki*. The effect of these fishes on native faunal composition and their inability to survive in small containers, tree holes etc., which are ideal breeding sites of vectorially important mosquitoes, make them inefficient in controlling mosquito populations. On the basis of larvicidal efficiency, the ability to produce dormant eggs, the hatchability of dormant eggs after rehydration, faster developmental rates, and higher fecundity, various tadpole shrimp can be considered to

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be ideal control agents in temporary water bodies and rice paddy fields. Among various predators of mosquito larvae, the cyclopoid copepods are efficient, found naturally, are safe for human beings, and are also economical in their application. The mosquito larval selectivity patterns of many cyclopoids, their adaptability to variable aquatic environments which are ideal breeding sites for mosquitoes, their resistance to starvation, and their day-night prey detection ability using hydromechanical signals make them an ideal biocontrol agent. Therefore, there is a need to test the feasibility of cyclopoid copepods by putting them into operational use as eco-compatible means of biocontrol. <http://zoolstud.sinica.edu.tw/Journals/45.4/447.pdf>

Key words: Mosquito predators, Larvivory, Copepod, Dragonfly larvae, Vector control.

INTRODUCTION

Mosquito-borne diseases have been a major problem in almost all tropical and subtropical countries, and currently there are no successful vaccines against most such diseases. For years, mankind has been exploring various methods to combat threats from mosquito-borne diseases. Many synthetic insecticides are widely used for controlling adult and larval mosquito populations. However, the harmful effects of chemicals on non-target populations and the development of resistance to these chemicals in mosquitoes along with the recent resurgence of different mosquito-borne diseases (Milam et al. 2000) have prompted us to explore alternative, simple, sustainable methods of mosquito control. The eradication of mosquito flying insect stocks using adulticides is not a prudent strategy, as the adult stage occurs alongside human habitation, and they can easily escape remedial measures (Service 1983 1992).

Until recently, the ecological role of environmental managers has been more concentrated on preventing damage from pollution rather than proposing sustainable solutions to different global and local problems faced by human societies. One of the multiple possibilities of applying ecological theories for human welfare is the use of our knowledge about the effects and mechanisms of predation and competition within various kinds of permanent and temporary aquatic habitats. By manipulating particular trophic levels, desired changes can be achieved in a system (He et al. 1994). Biotic interactions such as competition and predation have been reported to be capable of regulating the number of mosquito populations by reducing the number of larvae that survive through larval development and by increasing the larval and pupal duration times (Knight et al. 2004). It is obvious that different pathogens and disease vectors are part of the ecosystem, and anthropogenic alterations of natural conditions provide an advantage to some of these pathogens and disease vectors. The recent resurgence of various mosquito-

borne diseases may have been an indirect result of such altered conditions. Programs to decimate mosquito populations by trying to kill the adult stage frequently fail, because the adults reside alongside human populations in their households, and hiding places can often not be detected as refuges for mosquitoes, thereby allowing them to escape remedial measures. Even larval mosquitoes live in places where they are difficult to find and kill: for instance, in old tires, trash, water tanks, and basically any container that holds water (Service 1983). Precautions also have to be taken not to contaminate drinking water supplies and water-transport containers with potentially harmful chemicals. Additionally, mosquitoes have developed resistance to frequently used pesticides making it even more difficult to control adult populations. Essentially, larval mosquito populations should be the first target of all control measures (Service 1992, Briegel 2003).

The potential for the use of genetics against mosquito-borne infection has recently been considered in vector control programs. Recent techniques to modify genes of mosquitoes are believed to be an appropriate interventional remedy against malaria and dengue fever. The main purpose is to produce a genetically modified strain of mosquito in the laboratory which does not serve as a carrier of disease and which is competitively superior in the natural habitat such that wild mosquitoes will eventually be replaced after the release of genetically altered mosquitoes in nature. However, there are several problems with this approach, and it is taking some time to turn the prospects of this technology into practical tools (Stiling and Cornelissen 2005).

Therefore, the exploration of more-effective and eco-friendly techniques to control mosquitoes seems to be very promising. Various organisms, known as natural biological control agents, can be utilized to control mosquito populations, thus avoiding the use of chemicals and harm to the environment in the process. It is desirable to use biological control agents that can adapt to mosqui-

to breeding habitats, are found naturally, and pose no danger to people (Rishikesh et al. 1988, Spielman et al. 1993). Biological control means the use of different kinds of living things, and/or their derivatives to eliminate pest populations. Many biological control agents disperse by themselves enabling them to spread and build up viable populations (Caltagirone 1981, Bellows 2001, Headrick and Goeden 2001). In the field of applied ecology, there have been many attempts to achieve the biological control of pathogens or vectors by introducing new effective natural enemies to their natural habitats (Arthington and Lloyd 1989, Headrick and Goeden 2001, Denoth et al. 2002). The efficient selection of effective natural enemies has become increasingly important for the success of biological control programs.

Microbial larvicides such as *Bacillus thuringiensis israelensis* (Bti) and *Bacillus sphaericus* (*B. sphaericus*) are gram-positive, aerobic (facultative anaerobic) entomopathogenic soil bacteria (Johnson et al. 1995, de Maagd et al. 1999, Bobrowski et al. 2002). Mosquito larvae ingest the microbial product which is composed of a dormant spore form of the bacterium and an associated toxin (crystalline protein inclusion produced by Bti during sporulation). The toxin acts as a stomach poison by binding to receptor cells present in the insect but not in mammals (Lacey and Undeen 1986, Neri-Barbosa et al. 1997, Bishop et al. 1999, Batra et al. 2000). Interestingly, its application destroys larval mosquitoes but spares predators if present in the water (Ohana et al. 1987, Chansang et al. 2004, Su and Mulla 2005). Very recently non-larvicidal effects of *Bacillus* formulations have also been recorded in various mosquitoes (Zahiri and Mulla 2002). Relatively lower numbers of egg rafts have been recorded in ovitraps treated with Bti and *B. sphaericus* than in controls, and furthermore, an adverse relationship was found between the *Bacillus* product concentration and oviposition (Zahiri and Mulla 2005). Contrary to this, a liquid formulation of Bti dispersed by ultra-low-volume technology in laboratory and field experiments did not affect the oviposition behavior of *Aedes albopictus* females (Stoops 2005). The parasporal proteinaceous toxin produced by Bti, however, is photolabile and destroyed by sunlight (Bernhard and Utz 1993, Cooping and Menn 2001). In mosquito breeding habitats, they are only effective for 1-4 wk after application (Jensen et al. 2000, USEPA 2005). In a recent study in Taiwan, Teng et al. (2005) recorded that the maximum duration of effectiveness of Bti in reducing the larval num-

ber was 1 wk after application in rice paddy fields. Essentially, frequent applications to each breeding site are required, thereby making it more expensive and rigorous (Amalraj et al. 2000). A fermentation product called spinosad, produced by the actinomycete, *Saccharopolyspora spinosa*, is another naturally derived larvicide (Williams et al. 2003). In a recent study in Antalya, Turkey, the mosquito species *Culex pipiens* was eliminated from septic tanks in 7 d after the application of spinosad at a concentration of 100 active insects (a.i.)/ha (Cetin et al. 2005). This has been shown to be less toxic to birds and mammals (Bret et al. 1997, Breslin et al. 2000), and no adverse effects were detected on predatory insects such as ladybirds, lacewings, big-eyed bugs, or minute pirate bugs (Cooping and Menn 2001, Williams et al. 2003). Its applicability has not been assessed in nature. Many mosquito larvae have been reported to ingest toxic and noxious algae (mostly cyanobacteria) which inhibit larval development and decrease survival (Marten 1986); however, mosquito breeding sites are usually too dark for algal growth.

The fungus *Lagenidium giganteum* has been shown to have the ability to control mosquito populations through oospores that can resist drought and which can readily be produced in bulk. Oospores survive for many years in the soil, but can reactivate within only about a month after flooding. In practice, the spores are activated by remaining in wet for 1-2 wk before being sprayed on the surface of the site to be treated (Cooping and Menn 2001). The fungus infects and kills only a portion of larval target mosquitoes, as well. The level might not be sufficient to decrease the risk of human infection. Very recently in rice paddy field ecosystems in Taiwan, *L. giganteum* has been found to be effective for only 1 wk in reducing the number of larvae after application (Teng et al. 2005), thus necessitating frequent application of this product.

The use of mosquito parasites, for instance, protozoans and helminths, might be a possible way (Sweeney and Becnel 1991, Santamarina et al. 1999) to control mosquito populations. Oocysts of *Ascogregarina* (a protozoan parasite) release sporozoites that disrupt the gut wall of mosquito larvae (Beier and Craig 1985). For instance, *Ascogregarina taiwanensis* and *As. culicis* normally infect *Ae. albopictus* and *Ae. aegypti* respectively (Munsterman 1990). The mermithid nematode, *Romanomermis iyengari* Welch, is another mosquito larval parasite of *Anopheles* and *Culex* larvae

(Iyengar 1927) first reported in 1927 in the lower Bengal delta, India. The biocontrol potential of *R. iyengari* against *Aedes*, *Anopheles*, and *Culex* mosquitoes has been evaluated in field and laboratory experiments (Chandrasah and Rajagopalan 1979, Santamarina et al. 1996). Some recent studies have demonstrated the effectiveness of *Romanomermis* for mosquito control in Mexico (Santamarina et al. 1999, Pérez et al. 2004). The feasibility under field conditions has not been established.

Biological control of mosquito larvae with biological agents like competitors and predators is more convenient and alleviates the need for frequent chemical applications. Biotic interactions of larval mosquitoes with different predators and competitors in aquatic ecosystems are schematically illustrated in figure 1.

The selection of biological control agents should be based on their potential for unintended impacts, self-replicating capacity, climatic compati-

bility, and their capability to maintain very close interactions with target prey populations (Waage and Greathead 1988). They eliminate certain prey and sustain such environments (i.e., as when prey is introduced, they eat the prey) for long periods thereafter (Marten 1994a). However, this will only be possible if the predator possesses extraordinary search efficiency irrespective of the illumination situation in response to the emergence of prey. It is important to have a sound general knowledge of a predator's prey selectivity patterns and particularly of its mosquito larval selection in the presence of alternate natural prey (Arthington and Lloyd 1989, Arthington and Marshall 1999). In addition, the predator's adaptability to the introduced environment and overall interaction with indigenous organisms need to be considered prior to introduction (Denoth et al. 2002, Carlson et al. 2004). This paper presents a brief account of different predators of mosquito larvae and possible prey/predator interactions in aquatic ecosystems.

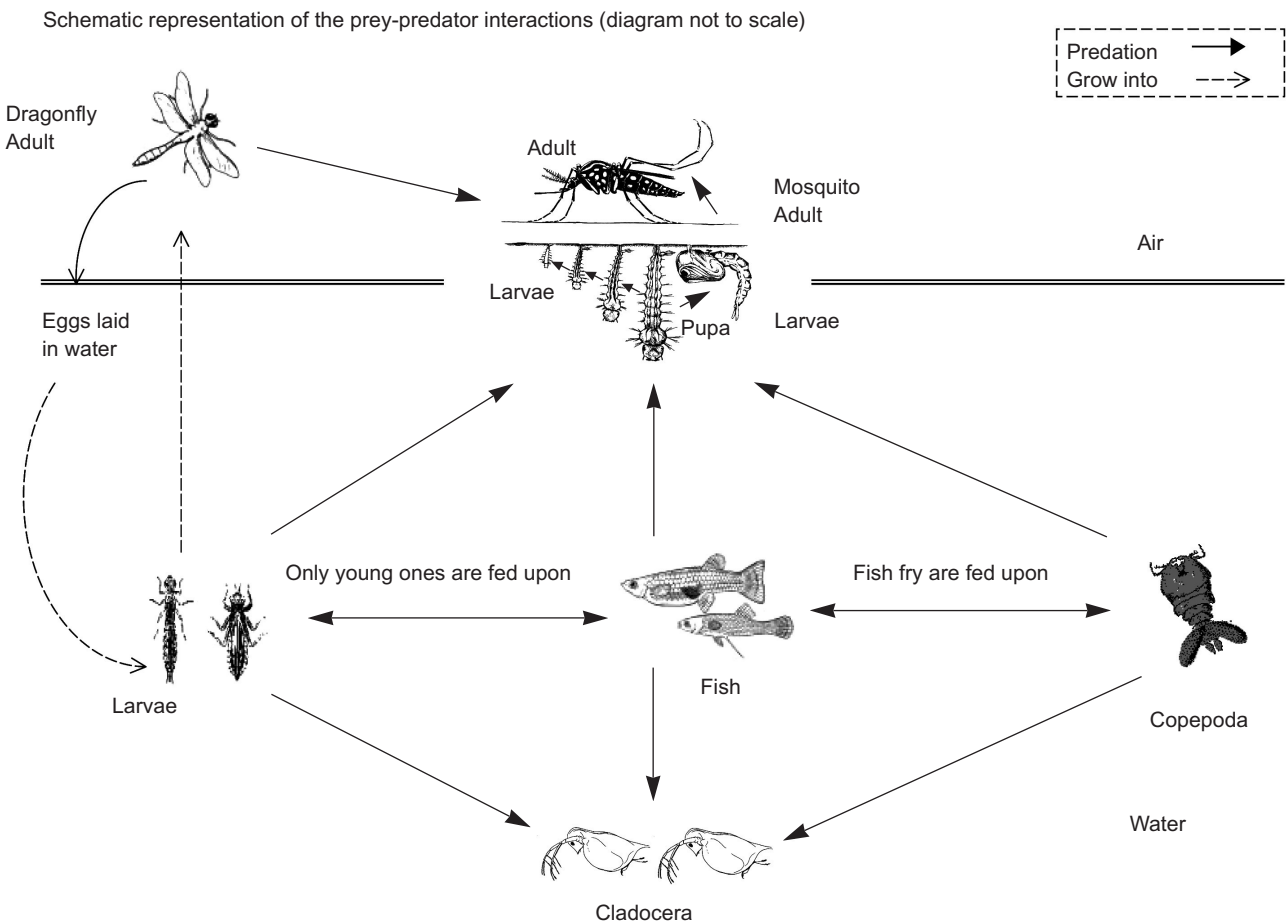


Fig. 1. Schematic representation of the interactions between mosquito larvae and their predators (diagram not to scale).

Amphibian tadpoles

Omnivorous tadpoles are potential predators of mosquito larvae (Spielman and Sullivan 1974, Morgan and Buttemer 1996, Webb and Joss 1997, Goodsell and Kats 1999, Komak and Crossland 2000) and exert significant impacts on freshwater ecosystems (Blaustein and Kotler 1993, Blaustein et al. 1996). Larvae of the giant Cuban tree frog (*Hyla septentrionalis*) have been reported to destroy aquatic insects and algae growing in water containers (Morgan and Buttemer 1996, Webb and Joss 1997, Goodsell and Kats 1999, Komak and Crossland 2000). However, the dietary niche breadth of larvivorous tadpoles includes other predators of mosquito larvae as well, hence they can efficiently predate on other co-occurring biocontrol agents of mosquito. Their efficiency in utilizing mosquito larvae in the presence of alternate prey has not been properly elucidated. It has been reported that tadpoles of *Rana tigrina* are more efficient mosquito pupal predators (Marian et al. 1983) than others. However, in nature, tadpoles are preyed upon by many predators, for example, mosquitofish (Grubb 1972, Gamratt and Kats 1996, Carwood 1997, Komak and Crossland 2000), catfish, and dragonfly larvae (Woodward 1983, Travis et al. 1985, Wissinger 1989). These predators prey on amphibian eggs and tadpoles, and contribute to substantial anuran declines (Baber and Babbitt 2003). Eklöv (2000) recorded that larval dragonfly, *Anax junius*, can utilize bullfrog (*R. catesbeiana*) larvae more efficiently than the bluegill sunfish (*Lepomis macrochirus*). Of course any introduction of amphibian tadpoles beyond their natural range is difficult and requires utmost caution. Tadpoles can rarely be accommodated in small containers that hold less than several liters of water and seem to have small impacts on larval populations of mosquitoes.

Larvivorous fish

One of the most widely distributed visually feeding fish is the western mosquito fish, *Gambusia affinis* (Baird and Girard), and the eastern mosquito fish, *G. holbrooki* (Giarard). During the 20th century, several fish species were introduced outside their natural habitats. Both, the western and eastern mosquitofish were introduced worldwide because of their reputation as mosquito-control agents (Krumholz 1948, Courtenay and Meffe 1989, Hammer et al. 2002). Both eastern and western mosquitofish possess a wide dietary

niche breadth. Feeding strategy analyses suggested high individual specialization, and thus an opportunistic feeding strategy for mosquitofish in both the juvenile and adult stages (Specziár 2004). They exhibit remarkable spatial and temporal variations, as the diet composition changes with the relative abundance of prey in the habitat (Cabral et al. 1998, Arthington and Marshall 1999, Willems et al. 2005). While mosquitofish have often been released in highly disturbed or artificial habitats, they have the potential to spread into pristine water bodies (Arthington and Lloyd 1989, Arthington 1991), where they severely impact native fish, amphibians, and invertebrates (Arthington 1991, Gamratt and Kats 1996, Howe et al. 1997, Webb and Joss 1997, Goodsell and Kats 1999, Leyse et al. 2004). Chinese health authorities have also used other fish species to exclude *Ae. aegypti* mosquitoes from breeding in large cisterns or other containers of drinking water. Small fish, such as *Claris fuscus*, *Tilapia nilotica*, and *Macropodus* sp. have been used in many regions to eliminate larvae in domestic water containers with considerable success. The use of catfish appears to be particularly effective (Neng et al. 1987). Larvivorous fish have been widely used as biocontrol agents of mosquito larvae, but they have their own limitations, for instance, such fish are expensive to rear and do not survive for long in small places (like containers, etc.).

Little is known about the ecology of larvivorous fish (Hurlbert et al. 1972, Hurlbert and Mulla 1981, Meffe and Snelson 1989). Comparative research on introduced and indigenous larvivorous fish feeding is particularly scarce, although it is crucial to determine the impacts of their introduction to ecosystems (Hoddle 2004). The mosquitofish has invaded relatively lower stream sections, mostly wetlands, shallow lakes, and almost all ornamental pools in different parts of the world. It has been shown that mosquitofish introduced in 1922 into southern California subsequently reduced populations of native fish throughout the state due to competition, predation, and hybridization. It has now become a threat to native fishes that share similar habitats, especially cyprinodontids because of its ecological advantages related to fast growth, early maturity, viviparity (Vargas and Sostoa 1996, Barrier and Hicks 1994), and food consumption, which can reach 83% of the fish's weight per day (Wurtsbaugh and Cech 1983). In addition to competition for resources, species of *Gambusia* are aggressive and often attack fish more than twice their own size and

mass (Gophen et al. 1998; Rowe 1998) which results in damage to the fins and scales, leaving the fish susceptible to disease. Considering its nontarget effects and extraordinary ability to spread in additional waters, ecologists have questioned the use of mosquitofish as biological control agents, especially when introduced as exotics to supplement native species (Moyle 1976, McKay 1984, Simberloff and Stiling 1996). The introduction of *Gambusia* into either riverine or large lake systems (Kolar and Lodge 2000) or in temporary and permanent wetlands (Leyse et al. 2004) can cause rapid declines in a variety of invertebrates, amphibians, and fish indigenous to those systems (Gill et al. 1999, Knapp and Matthews 2000, Hammer et al. 2002).

Some workers have used this species to test pelagic trophic interactions (Hurlbert et al. 1972, Lancaster and Drenner 1990), optimal foraging theory (Bence and Murdoch 1986), and toxicant bioaccumulation in wetlands. Some dietary studies have focused on its role in the control of insects (Linden and Cech 1990, Walton et al. 1990, Su and Mulla 2001). In nature, a wide spectrum of different foods is available. The utilization of target species by a predator depends upon its prey selectivity patterns in the presence of alternate natural prey co-occurring in the habitat with the target organisms. However, few studies have analyzed the dietary patterns of mosquitofish (Crivelli and Boy 1987, Specziár 2004). Since the beginning of the introductions, several studies have pointed out negative effects of mosquitofish on small indigenous fish species (Courtenay and Meffe 1989, Howe et al. 1997, Ivantsoff and Aarn 1999), amphibians (Morgan and Buttemer 1996, Webb and Joss 1997, Goodsell and Kats 1999, Komak and Crossland 2000), and invertebrates like zooplankton (Margaritora 1990), dragonfly larvae (Rowe 1987), damselflies (Englund 1999), and fairy shrimp (Leyse et al. 2004).

In natural habitats, many determinant factors which affect prey preference and the dietary niche breadth of *Gambusia* include the size of the water body, availability of food, population density, the invertebrate community, varieties of fish, primary production, water temperature, oxygen content, and the structure of sub-habitats (Mansfield and McArdle 1998). Recently Specziár (2004) recorded 34% algae, 19% detritus, and remaining animal prey in the gut content of *G. holbrooki*. In a study by García-Berthou (1999), animal food included 11% rotifers, 28% dipterans, 19% ostracods, 19% other insects, 18% copepods, and 5% cladocer-

ans. However, in another study on the eastern mosquitofish, *G. holbrooki*, of Lake Banyoles, Catalonia, Spain, it was observed that its diet was based on littoral cladocerans, particularly *Chydorus sphaericus*, *Scapholeberis ramneri*, *Ceriodaphnia reticulata*, and *Pleuroxus laevis*, and nematoceran (basically chironomid) adults. There was a large variety of prey of terrestrial (collembolans and ants) or aquatic neustonic origin (*Sca. ramneri* and emerging nematoceran adults), showing that the foraging range of microhabitats of the mosquitofish is closely linked to the water surface. Those studies, conducted in natural water bodies, did not record a significant amount of larval mosquito in the diet of mosquitofish. Prey preference by mosquitofish has not been found to be related to fish density (García-Berthou 1999). Significant differences in the extent of carnivory and efficiency of utilizing dipteran larval prey have also been reported between sexes. Sexual dimorphism and size play a very important roles in feeding behavior and differentially affect the utilization of food. Females generally predate more intensively over a wider range of items in response to their larger size and reproductive needs, while males and juveniles change their strategy to avoid competition and exploit resources (Specziár 2004). The optimal temperature for *Gambusia* feeding rates was 30-35°C (Specziár 2004). *Gambusia* has a voracious appetite, feeding at rates much higher than those of most other similar-sized fish. At optimal temperatures, maximum consumption rates ranged from 0.75% to 1.1% of body weight per day for fish ranging from 0.2 to 1.2 g (Cabral et al. 1998). Because of their ability to spread widely and their negative impact on aquatic communities, *G. affinis* and *G. holbrooki* have been designated among 100 invasive species worldwide (ISSG 2000).

Predator escape mechanisms in mosquitoes

Different oviparous insects have been reported to avoid aquatic sites where there is a high predation risk to their offspring. Mechanisms for predator detection by insects may involve tactile, visual, or chemical cues (Spencer et al. 2002). The proximate mechanisms that mediate avoidance behavior are certain chemical exudates released by predators that are commonly called kairomones. Chemically mediated avoidance is an adaptation used by prey to detect and evade predators. Kairomones or semiochemicals emitted from predators (Nordlund 1981) are normally used

by prey to detect a predator's presence in the environment, and the prey can thereby minimize such encounters (Kerfoot and Sih 1987, Kats and Dill 1998). Common responses to chemicals from predators include an increased use of refuges (Kats et al. 1988), marked changes in the intensity of movements (Mathis et al. 1993, Chivers et al. 1996, Huryn and Chivers 1999), reduced foraging (Petranka and Hayes 1998), reduced courtship behavior, predator avoidance (Flowers and Graves 1997), and increased growth rates (our own observations). Chivers and Smith (1998) and Kats and Dill (1998) reviewed studies showing that fish, amphibians, reptiles, mammals, a bird, and a broad array of invertebrates have evolved chemosensory mechanisms for detecting predators. Kats and Dill (1998) list 16 studies which involved larvae of aquatic species that provide evidence for chemically mediated detection of aquatic predators by insects. Where chemical cues are involved, responses to predators are often influenced by the predator's diet. For example, mayfly and damselfly larvae are more likely to respond to fish chemicals if the fish have recently consumed conspecific prey (Chivers et al. 1996, Huryn and Chivers 1999). Prey species are more likely to evolve chemically mediated avoidance of predators when visual detection of predators is limited (Kats and Dill 1998, Petranka and Hayes 1998). In turn, prey must possess suitable behavior and chemosensory mechanisms to detect and respond to predators. Mosquitoes appear to meet most of these requirements since many species are crepuscular or nocturnal and rely heavily on chemosensory mechanisms when selecting oviposition sites. After mating and taking a blood meal, a hemolymph-borne hormone triggers the female to begin searching for a suitable oviposition site and to become receptive to chemical signals from the site (Klowden and Blackmer 1987). Gravid females are known to spend some time flying around a water body apparently evaluating it as an oviposition site (Lester and Pike 2003). The main criteria in such a selection process are the presence of competitors, predators, and/or kairomones (Murdoch et al. 1984, Blaustein et al. 1995, Lester and Pike 2003) and container size (Angelon and Petranka 2002, Sunahara et al. 2002, Lester and Pike, 2003). Females oviposit on mud or the water's surface (e.g., *Culex* spp.) after sampling the chemical composition of the substrate using receptors on the tarsi, antennae, and tips of the proboscis (Davis 1976, Bentley and Day 1989). Published evidence convincingly suggests that

mosquitoes use chemosensory information to assess several parameters that reflect habitat quality for the offspring, including the availability of nutrients, the presence of competitors and predators, and the overall quality and permanence of the water body (Davis 1976, Angerilli 1980, Chesson, 1984, Bentley and Day 1989, Edgerly et al. 1998). It has been demonstrated that mosquitoes and phantom midges greatly reduced ovipositing rates in experimental pools that contained caged sunfish (*Lepomis*) that were not visible to ovipositing females. Grostal and Dicke (1999) demonstrated a similar behavior in acarine mites, suggesting that this phenomenon may occur across a diverse array of arthropods. Recently it has been convincingly reported that adult mosquitoes have the ability to sense the presence of *Gambusia*, and that mosquitoes reduce egg-laying rates in pools containing the odor of mosquitofish (Angelon and Petranka 2002). Those authors conducted an experiment to determine whether mosquitoes reduce oviposition rates in pools containing chemicals of the mosquitofish (*G. affinis*). Their experimental treatments consisted of outdoor pools that contained known concentrations of fish chemicals (low, medium, or high) or no fish chemicals (control). The mean number of larvae of the mosquito species *C. pipiens* per pool significantly differed in the experiment and was about 3 times larger in control pools compared with those containing medium and high concentrations of fish chemicals. That study clearly demonstrated that ovipositing female mosquitoes are able to make use of fish kairomones to make behavioral decisions that affect encounter rates of future offspring with predators.

In nature, *G. affinis* inhabits temporary habitats such as swamps, roadside puddles, and ornamental ponds, and forms schools that may contain hundreds of individuals. Schooling behavior produces a patchy environment where predation risks may vary locally, depending on the location of schools. Female mosquitoes avoid *Gambusia* at several spatial scales. For example, females can use the strength of fish chemicals to avoid local sites in ponds with dense schools. Alternatively, females might strongly avoid ponds with *Gambusia* and seek out ponds with fewer or no fish (Ritchie and Laidlaw-Bell 1994).

Moreover, recent reviews have not supported the effectiveness of the mosquitofish in controlling mosquito populations or mosquito-borne diseases (Arthington and Lloyd 1989, Courtenay and Meffe 1989, Rupp 1996). In some cases the mosqui-

tofish may even indirectly increase the survival rate of mosquito larvae by feeding on their cladoceran competitors (Blaustein and Karban 1990). Courtenay and Meffe (1989) concluded that despite its reputation as being an effective predator of mosquitoes, *Gambusia* is generally ineffective as a biological control agent. For example, *Gambusia* had a positive impact on controlling mosquitoes in only four of 20 countries where it was introduced for mosquito control or other purposes. One explanation for the ineffectiveness of *Gambusia* in controlling mosquitoes is that ovipositing mosquitoes may seek out fish-free habitats that adjoin large bodies of water containing *Gambusia*. The active avoidance of habitats with a high predation risk to offspring may ultimately act to sustain high densities of mosquitoes near areas stocked with *Gambusia*. Ritchie and Laidlaw-Bell (1994) found that ovipositing *Ae. taeniorhynchus* strongly avoided sites with high densities of *G. holbrooki* and shifted to adjoining habitats with few or no predatory fish. Similar results were obtained by other workers (Stav et al. 2000). Therefore, female mosquitoes often avoid ovipositing in waters containing predatory fish (Chesson 1984, Blaustein et al. 1995, Blaustein 1998, Angelon and Petranka 2002, Kiflawi et al. 2003a b). The limitations of *G. affinis* and *Poecilia reticulata* at controlling mosquito populations have been further proven in a comparative study conducted by Wang 1998, who revealed that the Taiwan native larvivorous fish, *Macropodus opercularis*, was better adapted to the breeding habitat and could control larval populations 8 times more efficiently than could *G. affinis*.

Therefore, recent studies suggest that the effectiveness of *Gambusia* in controlling mosquitoes may be compromised if adult mosquitoes respond to fish stocking by shifting to nearby breeding sites that lack fish. The use of *Gambusia* in biological control programs should be reconsidered.

Aquatic insects

Some aquatic insects play important roles in mosquito control (James 1966, Ellis and Borden 1970, Pandian et al. 1979). In general, almost all aquatic insect predators prey on mosquito larvae and pupae (Ellis and Borden 1970, Peckarsky 1984); the aquatic coleoptera (especially notonectids and dysticids) and odonates have been observed to ingest mosquito larvae as a part of their natural food assemblages. The

backswimmer, *Notonecta undulata* (Hemiptera, Notonectidae), has been shown to efficiently utilize the second instar of mosquito larvae as prey (Ellis and Borden 1970, Murdoch et al. 1984, Blaustein et al. 1995, Blaustein 1998). The role of the backswimmer, *Anisops assimilis*, in controlling mosquitoes was recognized as early as 1939, when Graham (1939) noted some stock troughs with *A. assimilis* were free of mosquitoes, whereas puddles in depressions surrounding the troughs contained "energetic mosquito activity". However, the predation efficiency of backswimmers on mosquito larvae was found to be container-specific (Lester and Pike 2003). For instance, diving beetle (*Rhantus pulverulosus*) and damselfly larvae are predators of mosquito larvae and show a preference for larger container sizes (Sunahara et al. 2002). Furthermore, the presence of backswimmers within a water body has been demonstrated to reduce oviposition rates by adult mosquitoes (Chesson 1984, Blaustein et al. 1995).

Larvivorous psorophora

Toxorhynchites, a kind of mosquito with cannibalistic larvae, has attracted much attention as biological control agents. Certain kinds of *Toxorhynchites* mosquitoes are good for the control of *Ae. aegypti* because they breed in the same kinds of containers. However, it proved to be unsuccessful in the field. Repeated release of *Toxorhynchites* 1st instar larvae in waterlogged places between bamboo trees had no effect on mosquito populations in Indonesia (Annis et al. 1989 1990). Ironically it was recognized that it increased prey density. This type of interfering effect became evident when the prey was present in excess (Hubbard et al. 1988). Subsequent tests and trials have obtained similar results (Annis et al. 1989 1990).

Odonate larvae

The order Odonata includes insects like the dragonfly and damselfly. They enjoy a wide distribution and are particularly prominent around aquatic ecosystems in tropical countries. Invariably the adults mate near water bodies, and the females lay eggs in water soon thereafter. Aquatic larval instars are predators of mosquito larvae. Dragonfly larvae, in particular, may be useful for controlling mosquito larval populations. In an experiment in Myanmar (Burma), 2 dragonfly larvae were introduced in domestic containers

accommodating *Ae. aegypti*. The mosquito larvae disappeared quite rapidly after dragonfly larva introduction to each container, and the density of target adults declined about 6 wk later. The dragonfly and damselfly are true enemies of mosquitoes as the larvae of these insects are able to utilize mosquito larvae as food, and the adults are efficient predators of airborne adult mosquitoes (Fig. 1). However, they not only consume large numbers of mosquitoes, in both larval and adult forms, they also predate on different zooplankton (gnats, midges, small moths, and little tadpoles; Travis et al. 1985) beetles, and other insects (Brendonck et al. 2002). Furthermore, Stav et al. (2000) evaluated the overall consumptive and non-consumptive (conditioned water) effect of the nymph of *Anax imperator* (Aeshnidae: Odonata) on populations of larval mosquitoes. They found no difference in the oviposition of the mosquito, *Culiseta longiareolata*. Still, the quantitative evaluation of consumption of mosquito larvae by odonate larvae in the presence of other prey is warranted. Breene et al. (1990) observed no mosquito larvae in the gut of larvae of the damselfly (*Enallagma civile*). Their analysis revealed that the larvae preyed upon chironomid larvae, and they also found corixids, cladocerans, ostracods, and aquatic mites. No remains of mosquito larvae were detected in any of the specimens, even though mosquito larvae (*Aedes*, *Culex*, *Culiseta*, *Mansonia*, and *Psorophora*) were observed in the pond where the damselfly larvae were collected (Breene et al. 1990).

Certain water bugs, e.g., *Sphaerodema annulatum* and *S. rusticum* (Heteroptera: Belostomatidae), are known to utilize mosquito larvae. Recently it was found, however, that the consumption of larvae by these bugs is dependent on the density of larval prey in the medium, so a considerable amount of mosquito larvae is likely to be left unconsumed (Pramanic and Raut 2003, Aditya et al. 2004 2005). None of these agents has shown any promise for mosquito control, as they have been proven difficult to rear and store, as well as being unstable or inefficient in the field. Their ability to aerially distribute themselves can be an advantage, as the adults have access to most, even tiny, water bodies where they lay their eggs. Therefore, their larvae can be found in small water tubs and tanks as well, ideal places where mosquitoes may breed. Further in-depth studies need to be done to assess the role of aquatic insects and their contribution to the control of mosquitoes.

Larvivorous organisms in temporary water bodies

Temporary or ephemeral aquatic ecosystems (pools, puddles, floodplains, etc.) are natural, endorheic bodies of water, which experience a recurrent dry phase of varying duration. In other words, temporary aquatic systems are those in which the entire habitat shifts from being available to unavailable to aquatic organisms, for a duration and/or frequency sufficient to affect the entire biota (Williams 1987 1997). Generally, the hydroperiod in ephemeral water bodies corresponds to the breeding periods of mosquitoes, and such bodies become ideal breeding sites for mosquitoes, particularly for the genera *Aedes* and *Anopheles* (Laird 1988). In intermittent puddles, the even-shorter permanence of the habitat makes it favorable to breed immature culicids as a consequence of the rare exposure to predators (Laird 1988, Sunahara et al. 2002). The composition and density of larval mosquito communities are strongly influenced by the ephemeral or permanent nature of the pools (Campos et al. 2004, Okogum et al. 2005). James (1961 1966) reported that immature mosquitoes are less exposed to natural enemies in temporary than in permanent ponds. The most important suspected invertebrate predators in temporary pools are turbellarians (Blaustein 1990, Blaustein and Dumont 1990), notonectids, diving beetles (Coleoptera), dragonfly larvae (Odonata) (Wiggins et al. 1980, Williams 1987 1997, Blaustein et al. 1995, Herwig and Schindler 1996, Spencer et al. 1999), and crustaceans, e.g., tadpole shrimp (Su and Mulla 2001). Turbellarians assume a particularly important position in ephemeral ponds, as they have the ability to produce resting eggs which can survive dry periods (Blaustein 1990). They are present and become effective within the first few days after rains begin to fall, while most other invertebrate predators become effective only later in the hydroperiod of individual pools or even at a later stage during the rainy season. The most important flatworm predators are species of *Mesostoma* that occur in a wide range of habitats (Blaustein and Dumont 1990). These species display a wide variety of predation mechanisms. Some species produce a kind of mucus that functions as a toxic web to trap and kill prey organisms (Dumont and Carels 1987). Other species just wait to attack the approaching prey (sit and wait or ambush predation). In addition, Dumont and Carels (1987) showed that

Mesostoma cf. lingua produces chemicals that are toxic to various prey organisms, e.g., *Daphnia magna*. Turbellarians have been observed to kill and utilize mosquito larvae as a food source (Blaustein 1990, Brendonck et al. 2002). Some species may also actively search for suitable prey (Schwartz and Hebert 1982) or reveal prey selectivity (Blaustein and Dumont 1990). Freshwater crustaceans, tadpole shrimp, and some copepods are adapted to temporary bodies particularly in arid zones. Besides direct consumption, tadpole shrimp have also been reported to enhance the efficacy of some microbial control agents like Bti. The digging activity and vertical foraging process of the shrimp in the water column facilitates the availability of Bti for larval feeding (Su and Mulla 2001). Basic quantitative data have not been reported in relation to mosquito larval selectivity patterns of these flatworms in the presence of other natural prey types (Schwartz and Hebert 1982, Blaustein 1990, Brendonck et al. 2002).

Cyclopoid copepods

Cyclopoid copepods are abundant in eutrophic water bodies and play important roles in their trophodynamics. Like many predators in aquatic environments, cyclopoid copepods are known to strongly influence the structural and functional organization of prey communities on which they feed (Kerfoot and Sih 1987, Matsumura-Tundisi et al. 1990, Irvine and Waya 1993, Plaßmann et al. 1997). Predominantly carnivorous but with an ability to utilize plants as well (Kumar and Rao 1999a b), cyclopids have a wide spectrum of potential food items available in their habitat, including algae, ciliates, rotifers, cladocerans, and copepod nauplii. The patterns of prey selection and feeding rates in this group of invertebrate predators have been the focus of considerable research (Greene 1983, Williamson 1986, Krylov 1988, Rao and Kumar 2002).

Some cyclopoids have long been known to have the ability to utilize mosquito larvae as food (Hurlbut, 1938, Fryer 1957, Brown et al. 1991a b, Marten 1990a b, Marten et al. 1994a b, Kay et al. 1992). Kumar and Rao (2003) conducted a series of behavioral observations of the cyclopoid *M. thermocycloides* handling and preying on mosquito larvae. Figure 2 shows the cyclopoid, *M. thermocycloides*, handling the larvae of *Culex quinquefasciatus*. In the laboratory, many species of *Mesocyclops* have been shown to prey upon *Ae. aegypti* or *Anopheles* larvae (Marten et al.

1994a b, Brown et al. 1991a b, Kay 1996, Kay et al. 1992, Mittal et al. 1997, Kumar and Rao 2003). Furthermore, in many ponds and small water bodies, a strong negative association has been reported between *Mesocyclops* sp. and larvae of *An. albimanus* (Marten et al. 1989, Zoppi De Roa et al. 2002). The ability of certain cyclopoid copepods to destroy larval mosquitoes was first noted in 1938 by Hurlbut. These "water fleas" were seen preying on newly hatched larvae. Field experiments in Rongaroa (French Polynesia) later demonstrated that *Mesocyclops* sp. can be used in interventions against *Ae. aegypti* (Rivière et al. 1987). Field trials have been conducted to determine whether copepods can usefully destroy larval *Stegomyia* mosquitoes. *Macrocyclops albidus* was released into each of about 200 tires arranged in 2 stacks of about 100 discarded tires each located near New Orleans (Marten 1990a b). A 3rd stack remained untreated. Larval *Ae. albopictus* that had been numerous in the treated tires at the beginning of the experiment virtually disappeared within 2 mo. Adults disappeared about 1 mo later and remained scarce for at least another year (Marten 1990b, Marten et al. 1994a b, Nam et al. 1998). These predators, however, did not reduce the abundance of the mosquito, *Culex salinarius*. Field trials are currently being conducted in different parts of the world to determine whether this is a good way of preventing the transmission of diseases. Preliminary results have been encouraging.

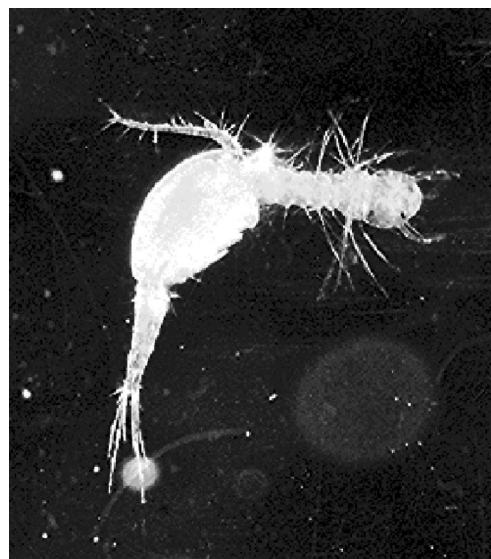


Fig. 2. Image of the cyclopoid copepod, *Mesocyclops thermocycloides* handling mosquito larvae of *Culex quinquefasciatus*.

Cyclopoids now appear to offer high promise as biological control agents for *Ae. aegypti* (Marten et al. 1994b), *An. stephensi* (Kumar and Rao 2003), and *Ae. albopictus* mosquitoes (Rey et al. 2004). Malarial mosquito larvae were found to be absent from aquatic habitats in Latin America (Marten et al. 1989) that contained natural populations of *M. longisetus* (Jennings et al. 1995, Nam et al. 1998, Marten et al. 1994a b) and virtually disappeared after *M. longisetus* and other species of *Mesocyclops* were introduced to rice fields and small marsh areas in Louisiana (Marten et al. 1994b). The technology using predatory cyclopoids for controlling mosquitoes is “appropriate” at modest costs. However, biological control using cyclopoids as predators against mosquito larvae has not received serious consideration in countries affected by mosquito-borne diseases.

An additional advantage of cyclopoids over other aquatic predators is that they are wasteful killers with the capability to kill more mosquito larvae than they actually ingest. If larvae are numerous, they eat a small part of each larva, which means that each copepod has the capacity to kill 30-40 larvae/d, far more than they actually eat (Kumar and Rao 2003). In natural water bodies, they are found in large numbers (Humes 1994). However, only about 10% of places with water where mosquitoes might breed contain natural populations of cyclopoids which can drastically reduce the survival of mosquito larvae (Brown et al. 1991a b, Kumar and Rao 2003).

However, not all copepods destroy all mosquitoes. Differential selection by copepods is related to mosquito larval species and instar stage (Fig. 3). Cyclopoids show distinct prey selectivity behavioral patterns and their prey selection patterns are influenced by many attributes of the prey such as morphology, behavior, and taste (Stemberger 1985, Rao and Kumar 2002, Kumar and Rao 2003). These are known to differ from species to species (Kumar and Rao 2001, Kumar 2005). Some species of cyclopoids usually select smaller prey items from the available prey size spectrum (Williamson 1980, Stemberger 1985, Kumar 2003), while others may actively select the largest prey they can capture (Krylov 1988, Janicki and DeCosta 1990, Rao and Kumar 2002). The extent of carnivory in omnivorous cyclopoids appears to be directly related to their body size (Fryer 1957, Adrian and Frost 1993). Animal prey selectivity of omnivorous cyclopoids has been demonstrated to be a function of their extent of dependence on an algal diet; for instance, some animals (e.g.,

Mesocyclops thermocyclopoides) can complete their entire life cycle exclusively on an animal diet, whereas others (e.g., *Cyclops vicinus*) have a food bottleneck in their life cycle (Adrian and Frost 1993, Kumar and Rao 1999b). The selectivity for animal prey in those species that include algae in their diet is also influenced by the extent of their dependence on algae (Adrian and Frost 1993, Kumar and Rao 1999b). In the laboratory, Kumar and Rao (2003) studied the prey consumption rates of the most abundant cyclopoid copepod in tropical and subtropical water bodies, *M. thermocyclopoides* on 1st and 4th instar larvae of 2 species of mosquito (*An. stephensi* and *C. quinquefasciatus*) in relation to their densities. Since prey vulnerability is a product of prey encounter rates with and ease of capture by the predator (Pastorok 1981, Kumar 2005), certain morphological and behavioral attributes of different prey species that determine capturability (Williamson 1980 1983), and their relative proportions (which

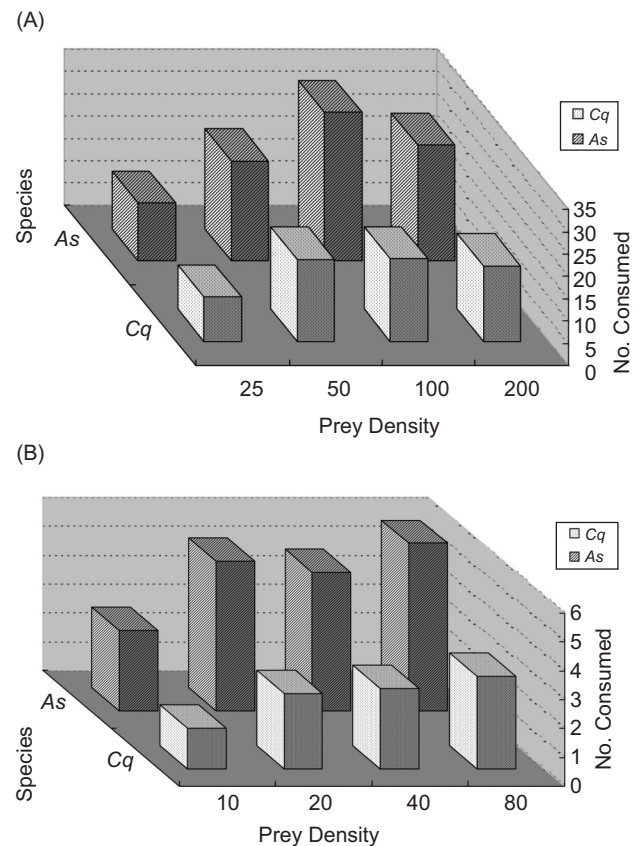


Fig. 3. Daily *per capita* prey killing rates (mean \pm SE) of *Mesocyclops thermocyclopoides* in relation to the larval density of the 2 mosquito species *Anopheles stephensi* (*A. s*) and *Culex quinquefasciatus* (*C. q*), (A) Instar I and (B) instar IV (Source: Kumar and Rao 2003).

affect encounter rates) in the medium may be able to explain observed differential larval selectivity patterns in copepods. Considering this point, Kumar and Rao (2003) also studied the prey selectivity of *M. thermocycloides* towards mosquito larvae in the presence of alternate prey (the cladocerans, *Moina macrocopa* and *Ceriodaphnia cornuta*) in different proportions. That laboratory study demonstrated that *M. thermocycloides* had biocontrol potential against *An. stephensi* even in the presence of alternative prey. However, against *C. quinquefasciatus*, there was a significant reduction in larval consumption in the presence of *M. macrocopa*, but not in the presence of either *D. similoides* or *C. cornuta*. The predaceous behavior of *M. thermocycloides* against mosquito larvae was comparable to that of *M. aspericornis* and other cyclopoid species reported earlier (Brown et al. 1991b). When offered a combination of instars I and IV, the cyclopoid actively selected instar-I larvae, avoiding instar-IV larvae of both mosquito species regardless of their relative proportions in the medium, and with either instar I or IV, the copepod selected *An. stephensi* over *C. quinquefasciatus* (Fig. 3B; Kumar and Rao 2003). When prey choice included a cladoceran as an alternate prey, the copepod selected the cladoceran only when the other prey was instar-IV mosquito larvae. Their results point to the potential of *M. thermocycloides* as a biological agent for controlling larval populations of mosquito species. It should be noted that the surface area of the container is one of the determinants of the predator's efficiency of controlling larval mosquitoes (Sunahara et al. 2002, Lester and Pike 2003). Therefore, further studies are required to assess the role of *M. thermocycloides* against mosquito larvae breeding in containers and other small water-collecting coolers, tires, etc.

It is further advantageous that mosquitoes do not show habitat avoidance on the basis of infochemicals secreted by the copepod (Torres-Estrada et al. 2001). Recently, those authors demonstrated that gravid *Ae. aegypti* females were significantly more attracted to ovitraps containing copepods or to ovitraps containing copepod-conditioned water than the controls. They concluded that the copepod infochemicals may be responsible for attracting gravid *Ae. aegypti* females and may increase the number of potential prey for the copepod. Such attractants may play an important role in the surveillance and control of mosquito populations (Thavara et al. 2004). Additionally, the cyclopoid can further be used in combination with

Bti to obtain better results (Tietze et al. 1994, Chansang et al. 2004).

Although *M. thermocycloides* is dominant in different lakes and ponds, its population is limited at places where mosquitoes may breed. Therefore, mass culture of cyclopoids should be established, and active adult cyclopoids should be introduced to different mosquito breeding habitats. The life cycle of cyclopoid copepods and their ability to thrive on a wide spectrum of food organisms make mass production easy and inexpensive; furthermore, they are highly resilient and can function in open containers of any size or shape. Females are inseminated when entering adolescence, and no further contact with males is required to produce 150-250 eggs/wk for their lifespan that can last for several months (Kumar and Rao 1999a). For start-up cultures, cyclopoids are collected from local lakes or ponds (Kumar and Rao 1998), and cultures can be established using ciliate or rotifer diets. In an experiment with various diets, *Mesocyclops* achieved the highest total fecundity with mixed food including rotifers, cladocerans, and algae (Kumar and Rao 1999a). Many species of *Mesocyclops* with biocontrol potential against mosquito larvae are relatively easy to culture, to maintain, and to deliver to the target areas (Kumar 2003, Kumar and Rao 1998 1999a b, Marten et al. 1994b 2000, Rey et al. 2004). Some of the common container-dwelling mosquito species, such as *Ochlerotatus* (formerly *Aedes*) *notoscriptus*, prefer containers that are not exposed to direct sunlight, and this is only rarely found in containers such as stock troughs (Lee et al. 1982, Laird 1990 1995). Cyclopoid copepods can survive in and colonize such habitats whereas other predators are more likely to find larger habitat patches (Washburn 1995).

Among non-copepod crustaceans, notostracan tadpole shrimp and malacostracan prawn are predators of mosquito larvae. They constitute an important group on many floodplains (Collins 1998). The larvivory efficiency of prawn (*Macrobrachium* sp.) was first reported by Pruthi (1928) followed by Jenkins (1964). Different malacostracan species show differential potentials for predation on larval mosquitoes. For example, *Paratelphusa spinigera* and *Varuna litterata* (Pruthi 1928, Jenkins 1964) are more-aggressive predators than *Macrobrachium borelli* and *Mac. lamarrei* (Collins 1998). Malacostracan-imposed mortality on larval mosquitoes recorded by Collins (1998) was insufficient to consider these malacostracans to be potential biocontrol agents of mosquitoes in

nature (Collins 1998). Notostracan tadpole shrimp have been considered to be potential predators adapted to ephemeral aquatic habitats in arid regions and rice paddy fields (Maffi 1962, Su and Mulla 2002). Maffi (1962) demonstrated that *Triops granarius* had the ability to decimate *An. gambiae* larvae in temporary breeding sources around huts in a village in Somalia. The biocontrol potential of tadpole shrimp against mosquito larvae was recently evaluated (Tietze and Mulla 1991, Fry-O'Brien et al. 1994, Su and Mulla 2001 2005). The larvicidal ability of tadpole shrimp combined with their life history strategy (formation of resting eggs in sediments, egg hatching success on dehydration, faster developmental rates, and high fecundity; Fry and Mulla 1992) indicates that they may be a suitable candidate for mosquito larval control in ephemeral habitats (Fry-O'Brien and Mulla 1996, Su and Mulla 2002). Furthermore, tadpole shrimp were demonstrated to have the potential to enhance the efficacy of microbial control agents such as Bti for mosquito control as their digging activity and vertical foraging process in the water column facilitate the availability of Bti toxin particles to mosquito larval feeding (Fry et al. 1994, Fry-O'Brien and Mulla 1996). Su and Mulla (2001) collected useful information with respect to colonization, stocking, introduction in mosquito breeding habitats, and establishment of *Triops newberryi* for the biocontrol of immature larvae in ephemeral habitats. Furthermore, Su and Mulla (2005) recorded negative effects of Bti, *B. sphaericus*, and larvicidal oil on the growth and survival of tadpole shrimp; however, the effect was dependent on the concentration.

Although highly promising, the practicality of these biological agents in anti-mosquito programs remains to be established. It has also been recorded that native fish (Courtenay and Meffe 1989, Wang 1998, Willems et al. 2005) and cyclopoid copepods (Marten 1994a b), including those that mosquitofish affect in their natural habitats, are better and more-efficient control agents. Therefore, the use of native fish, cyclopoid species, and tadpole shrimp (in temporary aquatic habitats) needs to be promoted.

CONCLUSIONS

Interventions targeting vectors of diseases are essentially the most effective strategies to control vector-borne diseases. Furthermore, a promising strategy would be to eliminate the aquatic juve-

nile or larval stages of vectors rather than the infective adult stage. Much of the current efforts directed at the development of new mosquito control tools are confined to the laboratory scale (Spielman et al. 1993). This type of research lacks good prospects for managing mosquito-borne diseases in areas of intense transmission. The major requirement of a program that will help stop the transmission of mosquito-borne diseases is the ability to adapt to various water bodies that are scattered within and around human settlements where vectorially important mosquitoes predominantly breed. As an example, a hidden automobile tire or a broken or unused container in the bathroom presents an obstacle to any effort in a society that respects privacy. Only biological agents carry the potential for overcoming such obstacles, and the most likely agents are those represented by closely related organisms. Toward this end, we require a program of biological research aimed towards understanding the factors that limit the number of mosquitoes. The search efficiency of the introduced predator and prey selectivity patterns of larvivorous organisms need to be explored by offering mosquito larvae in combination with other alternate natural prey. Care needs to be taken in case the introduced predator preys on or alters populations of indigenous flora and fauna of an ecosystem. Establishing a biocontrol agent requires an understanding of the mechanisms by which a predator directly or indirectly affects the community composition. This is also important for understanding under what set of environmental conditions a predator will be effective in reducing mosquito populations. Sometimes the presence of predators may cause a relaxation of intra- and interspecific competition. If the predator's negative effect on the larval population via consumptive effects of reduced intra- and interspecific competition is outweighed by its positive non-consumptive effects of reduced competition, then the introduction of larval predators might result in more rather than fewer mosquitoes. Nutrient regeneration caused by larval predators is another positive non-consumptive effect which may negate the consumptive effects. The success in measuring the efficacy of candidate agents depends on a multitude of factors: (i) characterization of natural enemy candidates including ecological, morphological, taxonomical, or genetic markers; (ii) selection of climatically matching candidates; (iii) evaluation of semi-field or field cage conditions following quarantine evaluations prior to proceeding with natural release; (iv) assessment of unintended

impacts; and (v) the potential efficacy of existing indigenous agents against larval populations.

A combination of life history, population dynamics, production, and eco-ethological traits (e.g., fast growth, reduced longevity, viviparity, high productivity, an intermediate position within the food chain, plasticity and adaptability in its food use, and no particularly special habitat requirements for reproduction) show that *Gambusia* introduced into different water bodies around the world may certainly produce important impacts on the structure and functioning of native biological communities. It is extremely important to reinforce the recommendations that *Gambusia*, the backbone of biocontrol for 1/4 of a century, should not be introduced into new areas. Mosquito larvae are rarely found in permanent waters, the sort of habitat where *Gambusia* flourishes. They are not likely to find their way to common mosquito breeding grounds such as tree holes, old tires, tin cans, undrained swimming pools, and boats. These, however, can be suitable habitats for invertebrate predators like cyclopoids and aquatic insects. Specific biological control agents for specific life stages of the mosquito can be used to ensure better and more-effective controls. Therefore, it is recommended that biological control agents be used that are effective even in such hidden places. Those found naturally are safe for people and are economic in their propagation. Turbellarians, cyclopoid copepods, aquatic insects, and native fish may prove to be more promising for controlling mosquito populations. The relative efficiency of various cyclopoid copepods in different ephemeral and permanent mosquito breeding habitats, and the introduction of larvivorous cyclopoids in combination with other entomopathogens such as Bt need to be evaluated before being used for effective mosquito biocontrol.

Acknowledgments: We are thankful to Prof. T. R. Rao, Univ. of Delhi, for constructive discussions and particularly his expert help with the photography of *Mesocyclops thermocyclopoides* capturing mosquito larvae. We immensely benefited from comments and suggestions made by Prof. H. U. Dahms, and 5 anonymous reviewers on a previous version of the manuscript. Thanks are due to Priyanesh Prasad and Li-Chun Tseng for bibliographic assistance. We acknowledge the National Science Council, Taiwan for providing a postdoctoral fellowship (0940020949 Dt.2005/03/10) to RK.

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