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EVALUATION OF COSTA RICAN COPEPODS (CRUSTACEA: EUDECAPODA) FOR LARVAL *AEDES AEGYPTI* CONTROL WITH SPECIAL REFERENCE TO *MESOCYCLOPS THERMOCYCLOPOIDES*

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ABSTRACT. This study attempted to find organisms for the biological control of the mosquito *Aedes aegypti* in Costa Rica. Copepods of the genera *Arctodiaptomus, Eucylops, Mesocyclops, Megacyclops,* and *Thermocyclops* were collected in several parts of the country and cultured for laboratory evaluations. *Mesocyclops thermocyclopoides* was the most successful species in reducing the number of larval *Ae. aegypti* (7.3 larvae in 24 h at a density of 200 *Aedes*/liter). *Arctodiaptomus dorsalis, Eucyclops* cf. *bondi, Eucyclops leptacanthus, Megacyclops* sp., and *Thermocyclops decipens* were not effective predators. In cage simulation trials, *M. thermocyclopoides* showed 100% larval reduction after 4 wk and adult mosquitoes disappeared after 7 wk. The copepod was able to survive in *Aechmea* sp. bromeliads under laboratory conditions. In field trials under 3 different climatic conditions *M. thermocyclopoides* survived 2–5 months in bromeliad leaf axils and 3–6 months in used car tires. In tires, this species reduced the number of larval *Ae. aegypti* 79, 90, and 99% in tropical dry, moderate, and humid climates, respectively. An El Niño phenomenon affected the results by drought, which apparently also caused a decline in the population of the predatory mosquito *Toxorhynchites haemorrhoidalis superbus.* Considering these severe test conditions, *M. thermocyclopoides* might be a promising predator for mosquito control in Costa Rica.

KEY WORDS Mosquito control, copepods, *Mesocyclops thermocyclopoides, Aedes aegypti,* El Niño, *Toxorhynchites haemorrhoidalis superbus,* dengue, Costa Rica

INTRODUCTION

From 1994 to 1997 the Ministry of Health in Costa Rica reported more than 40,000 confirmed cases of dengue, including 1 death due to hemorrhagic fever in 1997 (total population: 3 million people). The vector *Aedes aegypti* (L.) has infested all urban areas of the country despite intense insecticide applications and breeding site reduction campaigns.

Vector control with insecticides may cause environmental damage and mosquito resistance (Breakley et al. 1984). For this reason, the biological control of *Ae. aegypti* is an alternative or additional control measure that should be considered in some cases.

The predatory behavior of copepods on mosquitoes has been previously reviewed. Kay et al. (1992) evaluated *Mesocyclops* species from Brazil for their potential. Marten et al. (1994a) observed that *Macrocyclops albidus* Jurine and *Mesocyclops longisetus* Thiébaud were able to reduce numbers of *Ae. aegypti* larvae by more than 99%. Also, the copepods were able to survive in discarded car tires that are a typical habitat for *Ae. aegypti.*

The reproduction of copepods is easy and inexpensive (Suárez et al. 1992), so they could be utilized in countries suffering from mosquito-borne diseases. These crustaceans can survive for long periods of time in artificial containers (Marten et al. 1994b). Therefore, this method of control offers a very long-lasting prevention that saves resources that are usually spent on expensive insecticides.

Collado et al. (1984) collected *Mesocyclops thermocyclopoides* Harada in Costa Rica. The predation rate of this species on *Ae. aegypti* is less than that observed in *Mesocyclops longisetus,* found in Honduras (Marten et al. 1994b), but *M. longisetus* has not been reported in Costa Rica (Collado et al. 1984). For this reason, it seems necessary to search for *M. longisetus,* evaluate the potential of other species, and analyze the posibility of using *M. thermocyclopoides* in *Ae. aegypti* control, if *M. longisetus* can not be found.

This article describes the search for copepods in Costa Rica, their cultivation under laboratory conditions, and their predatory effects on *Ae. aegypti* under laboratory and field conditions. Additionally, observations on the survival of copepods in natural breeding containers such as bromeliads were made because they can be of importance in some cases, as was observed by Chadee et al. (1998). Because Costa Rica has a very diverse climate with tropical humid, dry, and more moderate areas, experiments were done in zones with different meteorologic characteristics that also can be observed in many other dengue-endemic areas of the world.

MATERIALS AND METHODS

Sampling: Copepods were sampled from reservoirs, lakes, artificial ponds, small natural ponds, fish farms, artificial fishing sites (sport fishing), rainwater accumulations, and stagnant water near rivers throughout Costa Rica. The specimens were collected using a plankton net (100-μm mesh size).

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Only the water close to the shore (3 m distance) was checked for copepods. Reid (1985) and Collado et al. (1984) were used for the identification of copepods. Voucher specimens were deposited at the Ministry of Environment (MINAE).

Culture: Copepods were cultured using the method of Suárez et al. (1992). A single gravid female was placed in a culturing solution containing *Paramecium* sp. and algae as food. At the beginning, small beakers containing 75 ml of solution were used. Fresh lettuce was added weekly. This organic material was then degraded by bacteria that could be consumed by *Paramecium,* which is an exellent copepod food source. When reproduction was successful, the animals were placed into a 2-liter beaker. The temperature varied between 22 and 26°C. The cultures were run with a photoperiod of 12 h, which is the natural daylight cycle in Costa Rica.

To avoid transmission of human pathogens, *Ae. aegypti* was cultured in an aquarium (40 × 30 × 30 cm) from larvae collected in used car tires in Heredia, a town without dengue reports. The immatures were fed on dry cat food pellets until they reached the pupal stage. The adults were fed on 100% saturated sugar water and a human blood source was offered 3 times per week. The females were allowed to lay eggs in a black container filled with water. For the predation trials, the eggs were removed and placed in 75-ml beakers until the larvae hatched.

Predation trials: The cultured copepods were placed in small beakers (1 individual per glass) containing 50 ml of chlorine-free water, after being starved for 24 h. Then, 10 larvae of *Ae. aegypt* (1st and 2nd instars) were placed into the beakers (density: 200 larvae/liter). After 24 h, the surviving larvae were counted. Ten replicates were conducted with each species. The same number of beakers with larvae but without copepods were used as controls. The temperature was maintained between 22 and 26°C. The results were analyzed statistically using Student's *t*-test.

Cage simulation: To observe the effects of the predation on the population of adult *Ae. aegypti* mosquitoes, 2 1 × 1 × 1-m cages were constructed. Two black plastic containers were placed in each cage, each containing 2 liters of water as a habitat for larvae. Dog food pellets were used as larval food. The adults were fed with a 100% saturated sugar solution. Once a week, a human blood source was offered. The methodology used was similar to that of Brown et al. (1991) and Kay et al. (1992).

The experiment was started with 20 larvae (2nd and 3rd instars) in every container (40 per cage), simulating a typical population found in artificial containers. The plastic containers in 1 of the cages were treated with 20 copepods each, whereas the cage without copepods was used as a control. The populations of adults, larvae, pupae, and copepods were recorded weekly. Air temperature varied between 23 and 30°C.

Survival in bromeliads: Bromeliads of the genus *Aechmea* were collected on the slope of the Barva Volcano, Heredia Province, and mounted on a shaded wall using wire, enabling the removal of each plant during the experiment. After 2 wk, 10 copepods were placed into the leaf axils to test their ability to survive in this mosquito habitat. Once a week, the water retained inside the axils was poured into a plastic pan and then into a glass. The surviving individuals were counted by holding the glass against the sunlight and then they were returned to the bromeliad.

Field experiments: Three different study sites were chosen to test the most successful copepod species under field conditions. The EARTH (Agricultural University of the Humid Tropics) site was located at Guacimo, Limón Province, on the Caribbean side of the country at 10°12'45"N, 83°35'38"W. This area has high precipitation and temperatures during the entire year (25.3°C average temperature; 4,496 mm annual precipitation in 1997). The Santa Rosa National Park site was located on the northern Pacific coast in Guanacaste Province at 10°50'30"N, 85°35'00"W. This site is characterized by low precipitation, high temperatures, and a 6-month dry season from December to May (26.2°C average temperature; 1,089 mm annual precipitation in 1997). The Heredia site was located in the Central Valley 1,200 m above sea level at 10°01'N, 84°07'W. This area has a moderate climate (20.3°C average temperature; 1,687 mm annual precipitation in 1997). Temperatures are lower than at the other sites but a marked dry season occurs from December to April and high precipitation occurs during the rainy season. Secondary forest vegetation was present at each site. Two of the areas were close to cultivated land (EARTH and Heredia), whereas the Santa Rosa test site was in the neighborhood of a research station and the national park administration.

At each of these areas the following experimental design was set up: 20 used car tires (10 to be treated with copepods, 10 as a control), 20 bamboo pots (internodes; 10 to be treated with copepods, 10 as a control), and 20 bromeliads (10 to be treated with copepods, 10 as a control). In Heredia and EARTH plants belonging to the genus *Aechmea* were mounted with wire to trees about 1.5 m above the ground, so that each plant was removable for larval surveys. In Santa Rosa, *Tilandsia* sp. was used in the same way.

The copepods were placed into each container at the experimental sites 2 wk after the beginning of the rainy season (Heredia: April; Santa Rosa: June). At EARTH (almost continuous annual precipitation), the animals were introduced into the containers in April, after allowing the mosquitoes to colonize the experimental site for 2 wk. Every 2 wk, the population of mosquito larvae was counted by

Table 1. Copepod species found at different localities.

Date	Location, Province	Habitat	Copepod species
Sept. 4, 1996	Guapiles, Limón	Fish ponds	*Mesocyclops thermocyclopoides* Harada
Sept. 9–12, 1996	ACG[1], Guanacaste	Small natural pond, four rivers	*Megacyclops* sp., *Mesocyclops* sp.
Sept. 25, 1996	Guapiles, Limón	Fish ponds	*M. thermocyclopoides, Arctodiaptomus dorsalis* Marsh
Oct. 6, 1996	Santa Elena, Cartago	Lake	*A. dorsalis, Thermocyclops dicipens* Kiefer
Oct. 8, 1996	Arenal (Puerto San Luis), Guanacaste	Reservoir	*Microcyclops dubitabilis* Kiefer, *M. thermocyclopoides, Macrocyclops albidus* Jurine[2]
Oct. 22–24, 1996	ACG[1], Guanacaste	Five small natural ponds	*Megacyclops* sp.
Oct. 24, 1996	Cañas, Guanacaste	Natural pond	*M. thermocyclopoides*
Oct. 24, 1996	Arenal (La Fortuna), Alajuela	Reservoir	*M. dubitabilis*
Nov. 12, 1996	La Sabana, San José	Artificial pond	*A. dorsalis, M. thermocyclopoides*
	La Paz Park, San José	Artificial pond	*M. Thermocyclopoides*
Dec. 24, 1996	Rio Corobici, Guanacaste	River	*A. dorsalis*
Jan. 18, 1997	Grecia, Alajuela	Artificial pond	*M. dubitabilis*
Jan. 25, 1997	Cachí, Cartago	Reservoir	*M. thermocyclopoides*
Feb. 23, 1997	El Camún, Cartago	Sport fishing facility	*Eucyclops leptacanthus* Kiefer
Feb. 23, 1997	El Empalme, Cartago	Sport fishing facility	*E. leptacanthus*
March 28, 1997	Limon	Estuary	*M. thermocyclopoides, Eucyclops* cf. *bondi* Kiefer

[1] ACG, Guanacaste Conservation Zone.
[2] Identification not positive; based on only 1 damaged individual.

rinsing the accumulated water inside the tires, bromeliads, and bamboo pots into a pan. Determination to genus or species level was accomplished using stereomicroscopes. The number of copepods was estimated by concentrating the animals with a plankton net into a 0.5-liter beaker. The number of individuals present was estimated visually while holding the beaker against the sunlight.

The populations of *Ae. aegypti,* the copepods, and *Toxorhynchites haemorrhoidalis superbus* (Dyar and Knab), a naturally occurring predator species, were plotted. The data obtained were analyzed statistically using Student's *t*-test. Meteorologic data were recorded at each of the study sites.

Table 2. Mosquito larvae surviving predation of Costa Rican copepods. Ten *Aedes* larvae (1st and 2nd instars) were exposed to copepods for 24 h. The untreated trial with the same number of larvae served as a control.

Copepod	Treated (standard deviation)	Untreated (standard deviation)	*n*
Mesocyclops thermocyclopoides	2.7 (1.34)	9.7 (0.49)	10
Thermocyclops decipens	8.7 (1.25)	9.3 (0.67)	10
Arctodiaptomus dorsalis	9.3 (0.82)	9.3 (0.95)	10
Eucyclops leptacanthus	7.7 (0.67)	9.0 (0.82)	10
Megacyclops sp.	6.3 (3.3)	9.2 (0.79)	10
Eucyclops cf. *bondi*	9.0 (0.8)	9.0 (0.8)	10

RESULTS

Sampling

Nine species of copepods were found in a variety of sites. Because very little work has been done on Costa Rican freshwater copepods (but see Collado et al. 1984), a list of all species found is given in Table 1. *Mesocyclops thermocyclopoides* is a very common copepod in most parts of Costa Rica from 0 to 1,000 m above sea level. This species has been found in fish ponds, artificial lakes, estuaries, and lagoons. *Macrocyclops albidus* has been found in Arenal Lake in a temperate climate zone.

Culture

Most species, except *M. albidus, Mesocyclops* sp., and *Arctodiaptomus dorsalis* Marsh, reproduced under the conditions described above. In some cases, *M. thermocyclopoides* developed densities of 800 individuals/liter.

Predation trials

The species shown in Table 2 were evaluated for their predatory behavior against *Ae. aegypti.* The species *Microcyclops dubitabilis* Kiefer was considered to be too small to prey on mosquito larvae. For this reason, it was not included into this experiment. *Arctodiaptomus dorsalis* did not repro-

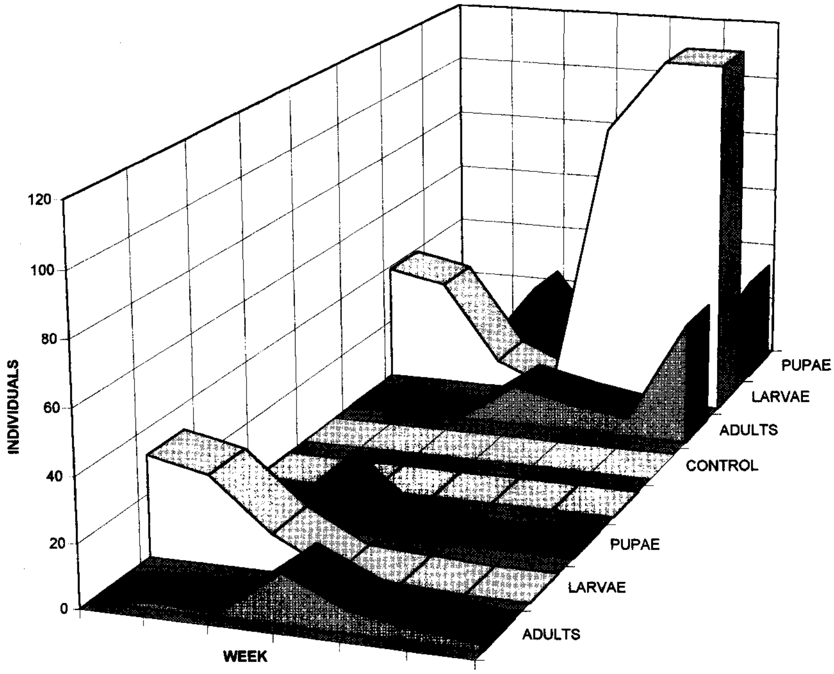

Fig. 1. Results of the cage simulation. Copepod-treated cages are in the lower part of the graph.

duce in the laboratory, so specimens from natural populations were used for testing.

Mesocyclops thermocyclopoides was the most successful predator. In the beakers with this species, a mean of 2.7 mosquito larvae survived predation. This reduction was significant at $P < 0.01$ (Student's t-test). The other species did not reduce the mosquitoes significantly. The survival of larvae was very similar to the control.

Cage simulation

Only the most successful copepod species (*M. thermocyclopoides*) of the former trial was evaluated in this experiment because the predation of the other species was considered to be too low. Most of the larvae introduced at the beginning of the experiment were able to develop to the adult stage because they were too large to be eaten by the copepods. After being bloodfed, these adults deposited eggs into the copepod-treated containers, but the hatched larvae were consumed by *M. thermocyclopoides* (Fig. 1). The effect of this copepod on the mosquito population was strong. After 4 wk, no more larvae were able to reach the adult stage. Seven weeks later, this had a measurable effect on the number of adults, compared with the control. Forty adult were present in the control; in the treated cage, only 2 adults were present. Also, in the control there were 34 pupae and 118 larvae were present at the end of the experiment, but in the containers with *M. thermocyclopoides, Ae. aegypti* was unable to develop. The results obtained in this experiment justified the use of this copepod species in field experiments.

Survival in bromeliads

Mesocyclops thermocyclopoides was able to survive in bromeliads as long as they contained water. During the experiment, some of the bromeliads dried out accidentally and the copepods died in most of these cases. In bromeliads with more than 100 ml of water, copepods survived in 5 of 10 plants (Fig. 2). When the water volume was lower than 100 ml no individuals survived because they were more likely to suffer desiccation. Gravid females and nauplii were observed in some cases; therefore, it can be assumed that *M. thermocyclopoides* was able to reproduce inside the leaf axils.

Field experiments

Mesocyclops thermocyclopoides was able to survive from 3 (Santa Rosa) to 6 (EARTH) months in tires and 2 (Santa Rosa) to 5 (EARTH) months in bromeliads. In Heredia, the copepods survived 3 months in bromeliads and 5 months in tires. At all sites, the population of copepods in tires varied considerably. The average number of individuals ranged between 18.2 and 389.3, with high standard deviations (Table 3). In bamboo internodes, no living copepods were observed after 2 wk, probably due to anaerobic conditions in the water accumulated inside. *Aedes aegypti* was not observed in the

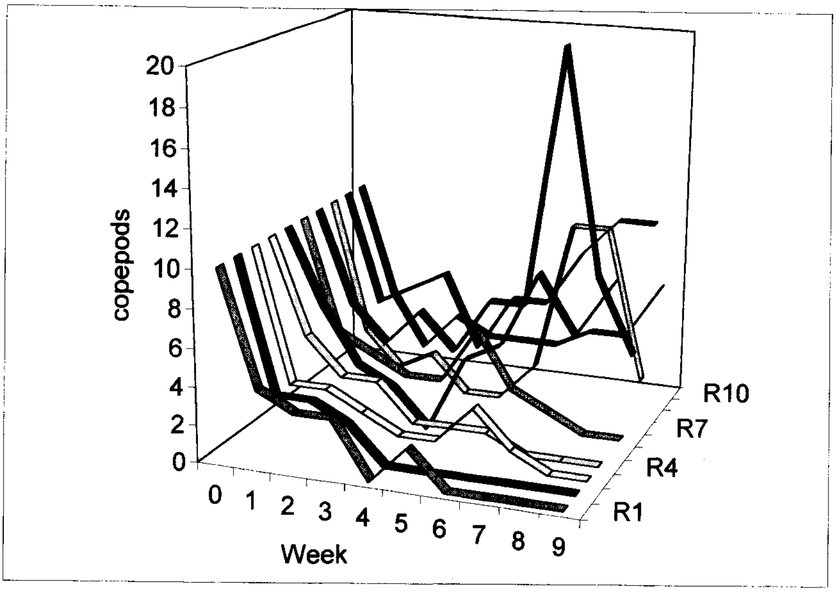

Fig. 2. Number of copepods surviving in bromeliads. Rows 1–4 contain less than 100 ml of water; the following rows contain 100–200 ml.

Table 3. Copepods surviving in tires and bromeliads at 3 different sites in Costa Rica from April 1997 to April 1998. Bamboo pots were not included because the crustaceans did not survive in these containers. See details in the text.[1]

	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April
Earth													
Tires													
Average	−20	23.5	29	28.5	43	48	28.3	ND	−20	117.1	83.3	201	389.3
SD	0	9.5	10	18.4	42.5	33.3	14.4		0	167.2	106.6	300	576.9
Bromeliads													
Average	−20	16.1	18.9	15.7	9.2	3.6	0	ND	0	0	0	0	0
SD	0	6.7	8.9	7.2	6.9	3.6	0		0	0	0	0	0
Heredia													
Tires													
Average	—	−20	18.2	ND	9	29.6	−20	38.7	32	23.3	—	—	—
SD	—	0	10.9		6.5	17.6	0	32	21.8	20.5	—	—	—
Bromeliads													
Average	—	−20	12.5	ND	5.4	0	0	0	0	—			
SD	—	0	8.6		5.4	0	0	0	0	—			
Santa Rosa													
Tires													
Average	—	—	−20	26.9	193.8	−20	50	74	52.5	—	—	—	—
SD	—	—	0	13.9	463.7	0	30.3	112.2	53.1	—	—	—	—
Bromeliads													
Average	—	—	−20	6.5	5	0	0	0	0	—	—	—	—
SD	—	—	0	1.7	0	0	0	0	0	—	—	—	—

[1] Average, average number of *Mesocyclops thermocyclopoides*; SD, standard deviation; −20, application with 20 copepods per container; —, container dry; ND, no data.

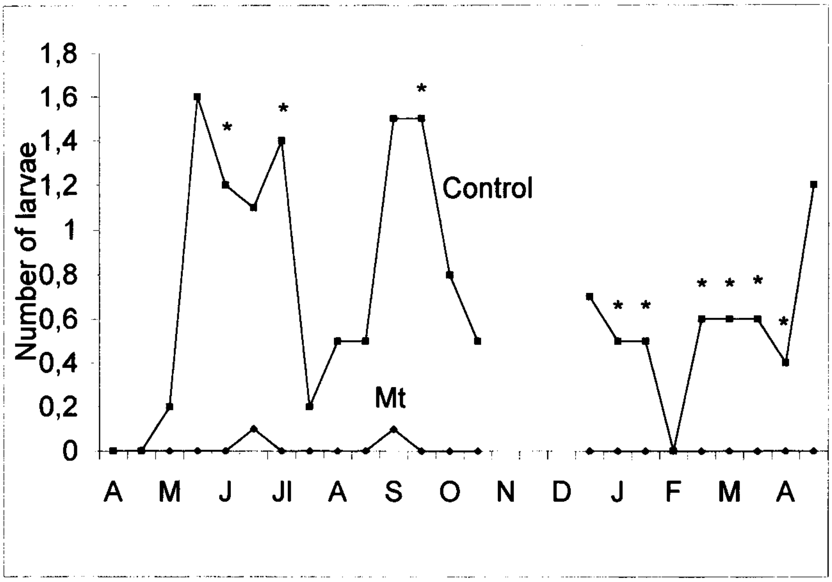

Fig. 3. EARTH: *Aedes aegypti* population in tires (April 1997 to April 1998). The asterisks (*) show significant differences in samples (*t*-test, $P = 0.05$). Mt = with copepods.

bamboo internodes, but was found in 2 occasions in bromeliads (Heredia and EARTH).

At EARTH, a 98.5% average reduction in numbers of *Ae. aegypti* larvae in tires was observed during the experiment. *Mesocyclops thermocyclopoides* was able to control the mosquito larvae nearly completely, but the number of individuals of *Ae. aegypti* was lower than at the other sites (Fig. 3). In November, most of the tires at the EARTH site were taken away by unknown individuals, so they were replaced. For this reason, the data records show a gap from November to December 1997.

In Santa Rosa, the tires dried out after 3 months due to low precipitation during July, August, and September (June: 287 mm; July: 65 mm; August: 32 mm; September: 171 mm; October: 286 mm), which was fatal for the crustaceans. After reapplying the copepods, the former level of control was achieved 1 month later (Fig. 4). The average reduction of *Ae. aegypti* in Santa Rosa was 79%.

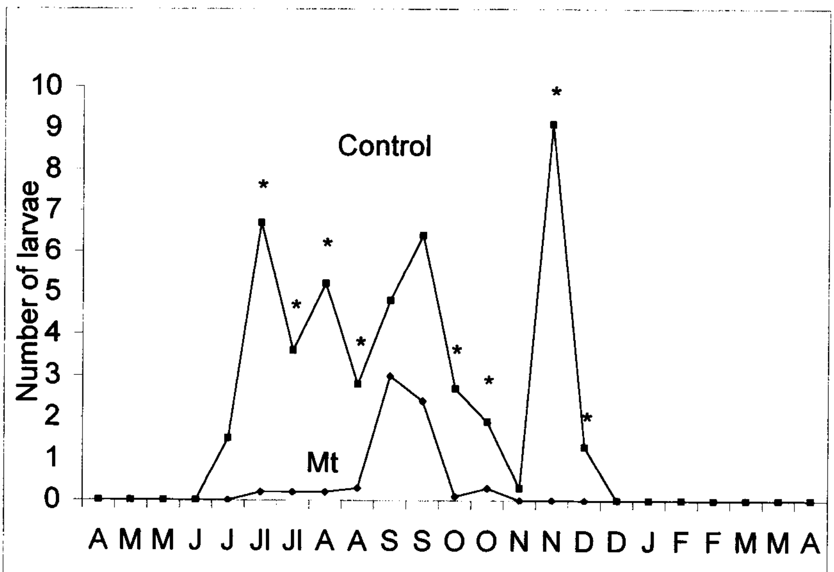

Fig. 4. Santa Rosa: *Aedes aegypti* in tires (April 1997 to April 1998). The asterisks (*) show significant differences in samples (*t*-test). Mt = with copepods.

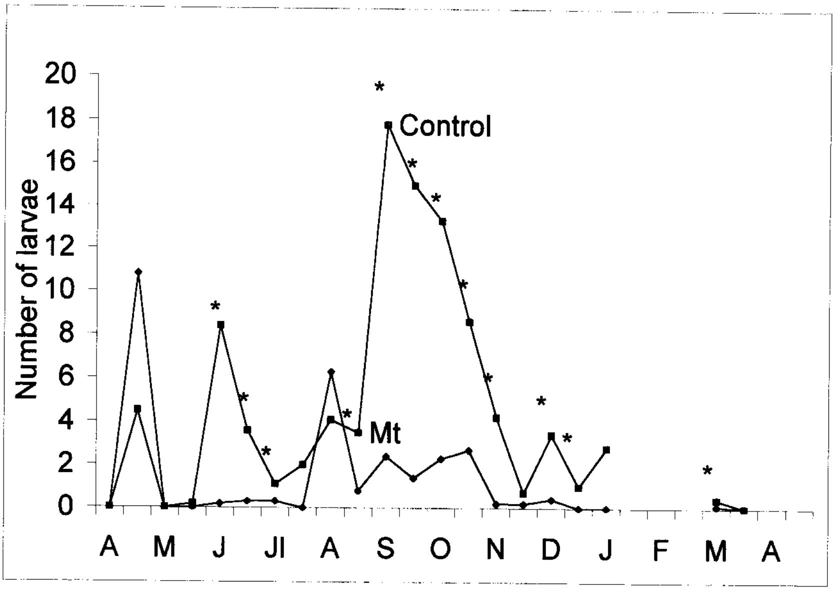

Fig. 5 Heredia: *Aedes aegypti* in tires (April 1997 to April 1998). The asterisks (*) show significant differences in samples (*t*-test). Mt = with copepods.

Also, the population of *Tx. haemorrhoidalis superbus* showed a strong decline in September (Fig.7).

At the beginning of the study, the crustaceans showed good survival rates in Heredia but the animals were probably killed by a herbicide application close to the experimental site in August. The number of *Tx. haemorrhoidalis superbus* larvae was reduced in the same period of time, probably due to the same cause. Nevertheless, this decline in the predator populations also correlated with a period of low precipitation (June: 254 mm; July: 40 mm). A reapplication was necessary in October 1997. Table 3 shows an average of 29.6 copepods inside the tires in September but 6 of the 10 tires did not contain any living crustaceans. The average reduction in *Ae. aegypti* was 90%. Figures 3–5 show the statistical significance of the reduction of *Ae. aegypti* obtained by Student's *t*-test.

The development of the population of *Tx. haemorrhoidalis superbus* can be seen in Figs. 6–8,

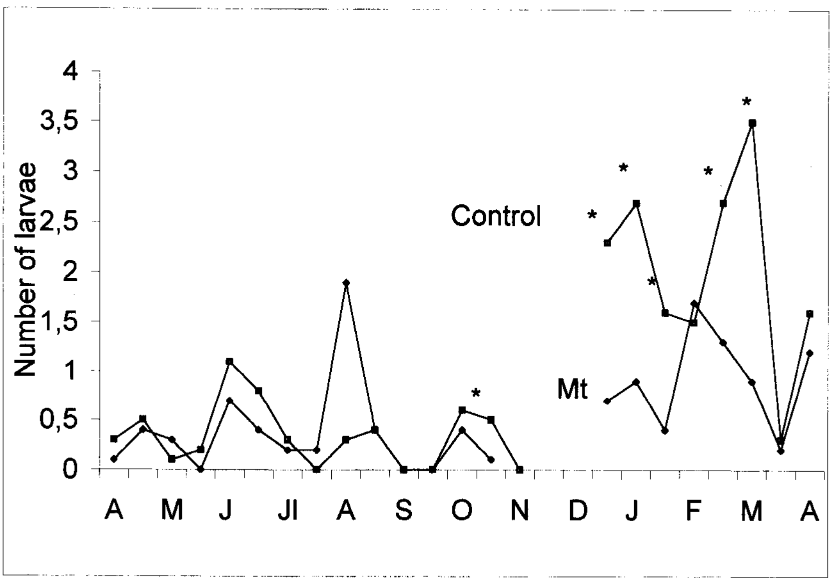

Fig. 6. EARTH: *Toxorhynchites haemorrhoidalis superbus* population in tires (April 1997 to April 1998). The asterisks (*) show significant differences in samples (*t*-test). Mt = with copepods.

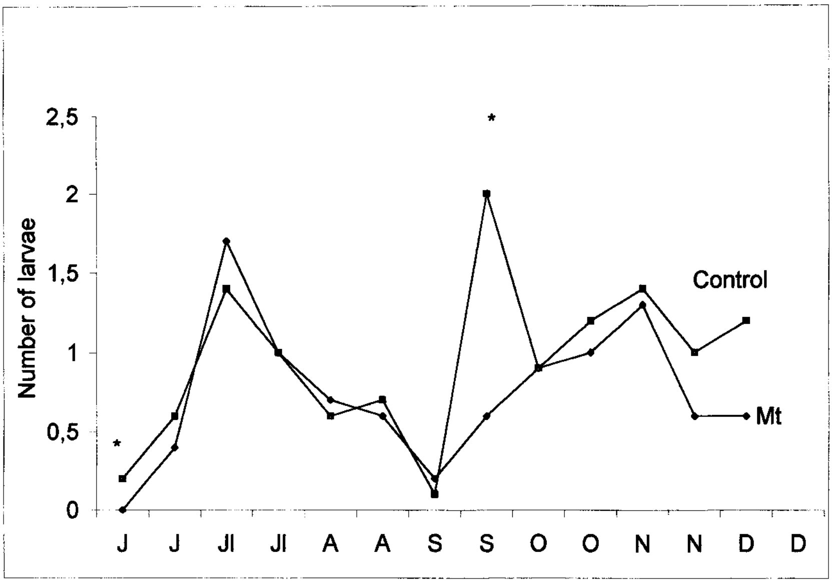

Fig. 7. Santa Rosa: *Toxorhynchites haemorrhoidalis superbus* population in tires (April 1997 to April 1998). The asterisks (*) show significant differences in samples (*t*tTest). Mt = with copepods.

which also show the statistical analysis of the reduction of this species by copepods. The number of *Toxorhynchites* larvae was 43, 39, and 22% lower in the copepod-treated tires at EARTH, Heredia, and Santa Rosa, respectively. This predatory mosquito showed strong populations at all sites, although the EARTH site had the highest number of individuals, specially from January to April.

DISCUSSION

The copepods *A. dorsalis, Megacyclops* sp., *Eucyclops leptacanthus* Kiefer, *Eucyclops* cf. *bondi* Kiefer, and *Thermocyclops decipens* Kiefer did not reduce the *Aedes* mosquitoes significantly, so *M. thermocyclopoides* is the only species having potential for mosquito control in Costa Rica. Marten

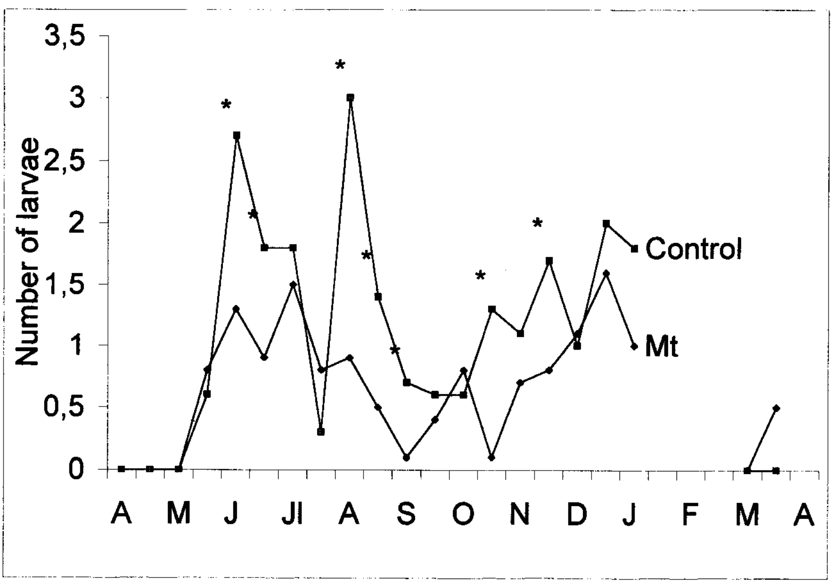

Fig. 8. Heredia: *Toxorhynchites haemorrhoidalis superbus* population in tires (April 1997 to April 1998). The asterisks (*) show significant differences in samples (*t*-test). Mt = with copepods.

et al. (1994b) showed that this copepod feeds on fewer larvae than *M. longisetus* and *M. albidus,* but *M. longisetus* has not been reported in Costa Rica (Collado et al. 1984; Table 1). *Macrocyclops albidus* has shown good levels of control but is not an appropriate species for mosquito control under tropical conditions because it does not resist high temperatures (Marten et al. 1997). In this study, *M. albidus* did not reproduce under the conditions mentioned above, perhaps because the individuals were exposed to high temperatures during transport. The same likely happened to *Mesocyclops* sp.

Mesocyclops thermocyclopoides had a broad distribution in Costa Rica and was, in fact, 1 of the most common species of this country. The distribution ranged from Guanacaste in the north to the Central Valley and the Atlantic coast of Costa Rica. *Mesocyclops thermocyclopoides* could be found in fish ponds, lakes, artificial ponds, and lakes, from sea level (Limón and Guanacaste provinces) up to elevations of 1,000 m (Central Valley). Similar observations about the biogeography and habitats of this species have been made by Collado et al. (1984).

In the cage simulation *M. thermocyclopoides* was very successful. After 4 wk, no more *Aedes* larvae were found. After 7 wk, the adult population collapsed due to natural mortality and lack of recruitment from larvae. Similar observations were made by Kay et al. (1992) on other *Mesocyclops* species.

This predator was able to survive in typical mosquito habitats. In field trials in Honduras, Marten et al. (1994b) observed a survival of 79% in drums for 30 wk. The bromeliad trials showed a reasonable survival. As long as the plants did not dry out, the animals survived up to 6 months in tires (EARTH). The survival of copepods in bromeliads might be important when *Ae. aegypti* is breeding in natural containers, as Chadee et al. (1998) reported in the Caribbean region. The authors reported larvae in calabashes, tree holes, leaf axils, bromeliads, coconuts, papaya stumps, rock holes, and ground pools. According to the present study, copepods might be a possible control method in natural breeding habitats, as long as they do not present anaerobic conditions, but more trials are needed to confirm this hypothesis.

The results of the field study show clearly the potential and the limits of the use of copepods for *Ae. aegypti* control. The long-term reduction of larvae in typical breeding sites is the most interesting observation made. As long as the experimental group was undisturbed, the copepods were able to maintain effective control of 90–99% of the mosquitoes in tires. Even in Santa Rosa, the driest experimental site, the crustaceans were able to control the larvae for 3 months. This exceeds the duration of control of *Bacillus thuringiensis* var. *israelensis* and methoprene, larvicides that usually worked from 2 to 4 wk (Tietze et al. 1994).

In 1997, the Central Valley and Pacific area suffered from unusually low precipitation, due to an El Niño phenomenon. During the months of June, July, and August the lack of precipitation at Santa Rosa was amplified by high temperatures (average temperature in August was 26.7°C, 1.2°C higher than in June). The consequence was a high mortality of *M. thermocyclopoides* in August because the tires dried out. After the resumption of the rainy season, the desiccation-resistant *Ae. aegypti* eggs were hydrated again and developed without any active predators present. In September, a reapplication of the copepods was necessary to continue the experiment. Other predators of the mosquitoes can be assumed to die because of the drought or high temperatures, which could explain the high prevalence of disease vectors in El Niño years. The number of *Tx. haemorrhoidalis superbus* larvae showed a strong decline in September, as can be seen in Figs. 7 and 8, indicating that this is one of the species that suffers reductions due to El Niño.

The long history of insecticide exposure of *Ae. aegypti* has resulted in resistance to many chemical compounds (Breakley et al. 1984). Copepods, on the other hand, have not been subject to pesticide applications and are thus very sensitive to chemical contamination. At the Heredia site, a herbicide application probably reduced the number of *M. thermocyclopoides* individuals considerably.

At all study sites a strong population of *Tx. haemorrhoidalis superbus* was observed, with the EARTH site being the site with the highest numbers of larvae found in the tires. As can be seen in Figs. 6–8, the number of *Tx. haemorrhoidalis superbus* larvae is up to 43% lower in the copepod-treated tires, probably due to copepod predation on the 1st instars of this mosquito, but this has not been confirmed. However, this reduction is considered not to affect the adult population of *Toxorhynchites.* Based on observations made on other *Toxorhynchites* species, the larvae of this species are probably cannibalistic (Annis and Rusmiarto 1988; on *Toxorhynchites haemorrhoidalis splendens*). This may be an important cause of larval mortality. As was observed in this study, only 1 or 2 larvae of *Tx. haemorrhoidalis superbus* reach the pupal stage in any tire, regardless of the presence or absence of copepods. Copepods and mosquitoes of the genus *Toxorhynchites* therefore seem to be compatible for *Aedes* control, an observation that also has been made by Brown et al. (1996). Also, the predation of the copepods on the mosquitoes might cause a deficiency of prey for *Toxorhynchites,* which might result in increased cannibalism. This might be another explanation for the lower number of larvae of this predator in treated tires.

The conclusion can be made that *M. thermocyclopoides* is a species of interest in the control of mosquitoes in Costa Rica, despite lower predation rates than other copepods, and considering also the severe test conditions during the El Niño year of 1997–98. To improve the impact on the *Ae. aegypti* population, combining the copepods with *Bacillus thuringiensis* var. *israelensis* and methoprene is also possible, to obtain better results (Tietze et al. 1994).

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