LIFE HISTORY EFFECTS OF PREY CHOICE BY COPEPODS: IMPLICATIONS FOR BIOCONTROL OF VECTOR MOSQUITOES

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ABSTRACT. *Macrocyclops distinctus, Megacyclops viridis,* and *Mesocyclops pehpeiensis,* which are common in rice fields during the summer season in Nagasaki, Japan, showed variable potentialities as biological control agents of larval *Aedes albopictus, Culex tritaeniorhynchus,* and *Anopheles minimus* in the laboratory. *Macrocyclops distinctus* and *M. viridis,* the largest copepod species, had fewer eggs within an egg clutch in nature than the smallest species, *M. pehpeiensis,* which also had a lower developmental time for sexual maturation (based on the appearance of the 1st clutch). Longevity as well as fecundity were influenced by nutritional conditions and varied significantly between the species. All species had shorter life spans when starved, but resistance to starvation was more pronounced in the larger species. Also, although all the species had lower clutch production when starved, although the frequency of clutch production was high in *M. pehpeiensis* (*M. pehpeiensis* produced a clutch every 2 days, whereas *M. distinctus* and *M. viridis* took on average almost 3 days), total clutch production was far higher in the larger species. The copepods fed readily on mosquito larvae, with *M. distinctus* and *M. viridis* killing fewer *Ae. albopictus* than *M. pehpeiensis,* which, however, killed fewer *An. minimus.* These copepods exhibited a similar and limited predation against *Cx. tritaeniorhynchus.* Results of our study support the contention that these copepods have the potential to be used as biological control agents of immature mosquitoes. Also, our results give useful information on colony maintenance and field introduction. In particular, releasing copepods with *Paramecium* as food could increase their survival in the habitat of the targeted pest.

KEY WORDS   Mosquito, immature, copepod, predation, reproduction

INTRODUCTION

Cyclopoid copepods are distributed almost universally in aquatic habitats and may occur at high densities in areas that produce mosquito larvae (Nasci et al. 1987, Brown et al. 1991). Although their interactions with mosquito larvae still are not fully understood, they have been demonstrated to serve as obligate hosts for fungi (Whistler et al. 1974, Frederici 1980) and microsporidia (Andreadis et al. 1985, Sweeney et al. 1985, Vossbrinck et al. 1998) to which mosquitoes are vulnerable. In addition, copepods have become a focus of large number of studies focused on their use for biocontrol (Riviere and Thirel 1981, Marten 1984, Nasci et al. 1987, Marten 1990, Marten et al. 1994, Zhen et al. 1994, Schreiber et al. 1996). Copepods have been shown to be very useful in controlling mosquitoes (*Aedes* sp.) in large containers (Nam et al. 2000, Kay et al. 2002) and in subterranean habitats (Russell et al. 1996, Kay et al. 2002). Presently, copepods are one of the most promising biological control agents.

Consideration of predatory efficiency, reproductive potential, ease of mass production, and survival is the 1st step of evaluating a candidate biocontrol agent. However, most of the evaluations of copepods as candidates for mosquito control have considered only their predatory efficiency on 1st-stage larvae. No evaluation has taken into account the reproductive biology of the candidate copepods, which is clearly directly related to their survival and ease of mass production in field applications. It has been reported that habitat desiccation (Zhen et al. 1994) and loss (Marten et al. 1994) have been reported to influence the populations of most species, including copepods. Disappearance of habitat was particularly noted when ecologically different species were mixed to improve control efficiency (Marten et al. 1994). Indeed, population loss is the most important factor limiting their use. Recently, Kay et al. (2002) reported desiccation resistance of eggs in the genus *Mesocyclops.* Therefore, a population ecological approach, especially one that includes the study of reproductive biology, should be involved in evaluating copepods as biological control agents.

In cyclopoid copepods, female reproduction is always sexual (Wyngaard and Chinnapa 1982, Gilbert and Williamson 1983) and ovigerous females carry their eggs in 2 sacs attached ventrolaterally to the genital segment of the urosome. When mature, the sacs drop and subsequently hatch within the medium (Gilbert and Williamson 1983). Females have 4 recognizable reproductive phases: ovigerous, bearing egg sacs; gravid, oviducts full of visible darkened matures oocytes; both ovigerous and gravid; and neither ovigerous nor gravid (Williams and Butler 1987). Females are able to store sperm, which enables the fertilization of many oocytes from 1 insemination (Hill and Cooker 1930, Williams and Butler 1987, Maier 1992). These alternative reproductive states depend largely on environmental factors, that is, food in particular (Williams and Butler 1987). Thus, diagnosis of the reproductive state is useful during a field trial.

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In this study, we evaluated 3 copepods (*Macrocyclops distinctus, Megacyclops viridis,* and *Mesocyclops pehpeiensis*) against 3 mosquito species from 3 genera (*Aedes albopictus* (Skuse), *Culex tritaeniorhynchus* Giles, and *Anopheles minimus* Theobald) by examining the reproductive output with reference to nutritional factors including starvation, mosquito prey, and the coexistence of *Paramecium.*

MATERIALS AND METHODS

Laboratory colonization, systematics, and basic features of copepods: The species used in this study were collected from rice fields near Isahaya City, Nagasaki Prefecture, in southern Japan. Sampled specimens were allowed to acclimate to the laboratory where they were maintained under controlled temperature (23–25°C) and light conditions and relative humidity (60–80%). Lighting was provided by 2 fluorescent tubes (80 W) with a 12:10 h light:dark photoperiod. From these samples, gravid females were introduced singly in trays and fed a mixture of *Paramecium–Chilomonas* infusion and boiled lettuce, following the methods of Suarez et al. (1992), to establish a monospecies culture. Copepod food was cultivated in plastic bottles and fed with wheat seeds. Cultures were renewed approximately weekly. Subsamples were made from laboratory-eclosed specimens for species identification, body size measurement, and counting of eggs.

Mosquitoes: A colony of *Ae. albopictus* was initiated from eggs collected in Nagasaki, whereas colonies of *Cx. tritaeniorhynchus* and *An. minimus* were initiated from larvae collected, respectively, from Nishi Arita and Ishigaki, southern Japan. Mosquitoes were maintained under the same environmental conditions as the copepods. Larvae were reared in trays, and fed daily with a mixture of liver powder and brewer's yeast. Adults were held in cages, provided with 10% sucrose solution, and bloodfed on mice at approximately 4–5 days after emergence.

Reproductive characteristics: From the colonies, 10 egg sac–bearing females of each species were placed in 250-ml vials filled with water and fed daily with 5 ml of a 7-day-old *Paramecium* infusion ($\sim 15.10^2$ cells, based on the method used by Enright and Hennessey [1987]). After egg hatch, parents were removed and nauplii were fed daily with 5 ml of mixed food (*Paramecium*:*Chilomonas* 2.5:2.5 ml). One week later, 2–3 progenies of each species that hatched on the same day were mixed to increase the chances of successful and viable mating.

Newly ovigerous females (with 1st clutch) were transferred individually into small vials under the same feeding conditions as their parents for fecundity and longevity studies. Fifteen to 18 of these females were assigned to 1 of 3 nutritional conditions: daily supply of 5 ml of *Paramecium* infusion (7-day-old); daily supply of live mosquito larvae; and starvation, given only tap water. The reproductive phase of each individual was recorded by daily observation under a lamp. In case of egg hatch, the experimental vial was washed with hot water to prevent an additional feeding source, because copepods are reported to feed upon their own nauplii (Maier 1995).

Predation on different mosquito larvae: The 3 copepod species were evaluated separately against 1st-stage larvae of *Ae. albopictus, Cx. tritaeniorhynchus,* and *An. minimus* in small vials with 5 ml of well water and 1 adult copepod that had been starved for 24 h. Larvae were given at a ratio of 50 larvae/copepod. Containers with the same number of larvae but without copepods served as controls. For each copepod, the predation trial against each mosquito was replicated 15 times.

Data collection: Following the method of Hopkins (1977), we measured the body size and the number of eggs contained in the 2 egg sacs (=clutch size) in laboratory-eclosed specimens. The distance from the nauplii eye to the end of the caudal rami, excluding setae, was used to represent body size. Clutch size was recorded after detaching both egg sacs and carefully dissecting the sacs by removing a protective membrane. In a predation experiment, mangled mosquito larvae were considered killed by copepods. The number of surviving larvae was counted after 1 day. The difference between the initial and final larval numbers was taken as the numbers killed per female per day. Reproductive parameters such as the time for the 1st clutch to appear (=sexual maturation time), the number of clutches produced, the interclutch period, and the age at death were monitored for each specimen. We calculated developmental time for sexual maturity as the time from maternal egg hatch to the appearance of the 1st clutch for each specimen. The interclutch period was the time between 2 clutches. Longevity was the time from maternal clutch hatch to death. Resistance to starvation was taken as the time from hatch to death in treatment without food.

Statistical analysis: The computer program Systat (Wilkinson 1996) was used to perform statistical analysis. A 2-way analysis of variance was applied to compare the basic features, developmental time, longevity, and resistance to starvation of the different copepod species as well as the number of mosquito larvae they killed. We analyzed fecundity and the effects of nutritional conditions on this parameter by comparing the numbers of clutches produced and the interclutch period (*Paramecium* treatment). The Tukey-test was applied for the comparison between copepod species in each of these parameters.

Table 1. Mean (± SE) body size (in mm) and clutch size in various copepod species.[1]

Species	Body size			Clutch size		
	Mean		Range	Mean		Range
Macrocyclops distinctus	1.57 ± 0.08 a	(*n* = 25)	1.47–1.75	26.04 ± 1.3 a	(*n* = 21)	14–37
Megacyclops viridis	1.53 ± 0.07 a	(*n* = 25)	1.37–1.67	65.92 ± 4.6 b	(*n* = 13)	33–101
Mesocyclops pehpeiensis	1.28 ± 0.07 b	(*n* = 16)	1.1–1.40	100.60 ± 4.9 c	(*n* = 15)	64–130

[1] By analysis of variance, values in the same column and with the same lowercase letter do not show a significant difference ($P > 0.05$); *n*, number of replicates.

RESULTS

Body and clutch sizes

These 3 species are significantly different in body ($P < 0.001$) and in clutch ($P < 0.001$) sizes. *Mesocyclops pehpeiensis* is smaller than *M. distinctus,* which in turn is smaller than *M. viridis* (Table 1). *Mesocyclops pehpeiensis* had more eggs within its sacs than *M. distinctus.* *Macrocyclops distinctus* had the smallest clutch size (Table 1).

Development and sexual maturation

This parameter differed significantly between species ($P < 0.0001$). *Mesocyclops pehpeiensis* had the shortest time to mating and extruding of the 1st clutch. It was followed by *M. distinctus,* whereas *M. viridis* had the longest time (Fig. 1).

Longevity and resistance to starvation

Both species and nutritional condition as well as their interactions significantly affected longevity
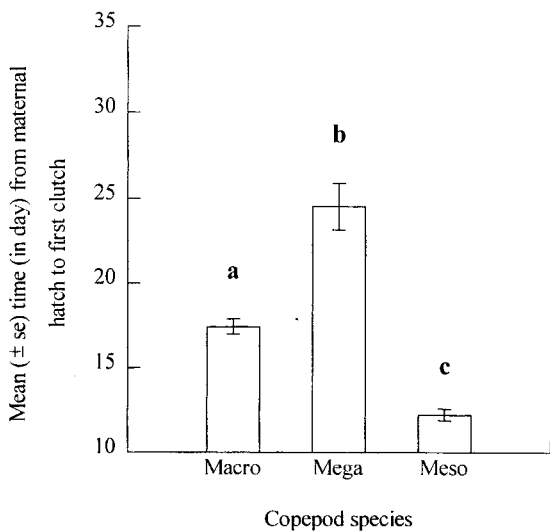

Fig. 1. Developmental time (in days) for sexual maturation of newly hatched nauplii of different copepod species when fed with a mixed *Paramecium–Chilomonas* infusion (Macro = *Macrocyclops distinctus,* Mega = *Megacyclops viridis,* and Meso = *Mesocyclops pehpeiensis*).

(Table 2). Life spans were different between the species for each nutritional condition ($P_{starvation} < 0.0001$, $P_{larvae} < 0.0001$, $P_{Paramecium} = 0.0159$). In all treatments, *M. pehpeiensis* had the shortest life span and *M. viridis* had the longest life span (Table 3).

Adult females of all species lived longer when supplied with either *Paramecium* or mosquito larvae than when starved ($P_{M. distinctus} = 0.0003$, $P_{M. viridis} = 0.0087$, $P_{M. pehpeiensis} = 0.0001$). Resistance to starvation was much higher in *M. viridis* and *M. distinctus.* *Mesocyclops pehpeiensis* had the same longevity when unfed or fed with mosquito larvae (Table 3).

Fecundity

A significant difference was found in egg sac production among the nutritional conditions (Table 2). In the starvation treatment, no significant difference was found in the number of clutches produced ($P_{starvation} = 0.1559$) between the species (Table 4). In copepods supplied with mosquito larvae, reproduction differed significantly between the species ($P_{larvae} = 0.0002$; Table 4). In the *Paramecium* treatment, although no significant difference was found in clutch production ($P_{Paramecium} = 0.1331$), *M. viridis* laid numerically more clutches than the other 2 species, in which the numbers of clutches produced were similar (Table 4).

Females of all 3 species produced the most clutches when fed ($P_{M. distinctus} = 0.0002$, $P_{M. viridis} = 0.0001$, $P_{M. pehpeiensis} < 0.0001$; Table 4). *Mesocyclops pehpeiensis* did not produce a single clutch in the absence of food, whereas *M. distinctus* and *M. viridis* females did produce clutches (Table 4). When food was supplied, all species reproduced, with *M. distinctus* and *M. viridis* producing the most clutches when supplied with mosquito larvae (Table 4). The timing of clutch production (when using only data from treatment with supply of *Paramecium*) was significantly different between species ($P = 0.0055$). *Mesocyclops pehpeiensis* had the shortest interclutch period (Table 5).

Predation

Larval mortality in containers with copepods was significantly different from that observed in control containers for each mosquito species ($P_{Ae. albopictus} < 0.0001$, $P_{Cx. tritaeniorhynchus} < 0.0001$, $P_{An. minimus} <$

Table 2. Results of analysis of variance for effects of species and nutritional conditions on longevity and egg production in various copepod species.

Source variables	df	Longevity F-value	Egg production F-value
Species	2	39.48*	11.47*
Starvation vs. larvae vs. *Paramecium*	2	17.17*	36.33*
Species × starvation vs. larvae vs. *Paramecium*	4	3.10**	4.39***

* $P < 0.0001$, ** $P < 0.05$, *** $P < 0.01$.

0.0001) and between species ($P < 0.0001$). No significant difference was found in number of larval *Aedes, Culex,* and *Anopheles* killed by *M. distinctus* ($P = 0.1228$; Table 6). However, larvae of *Ae. albopictus* were preyed upon most by *M. pehpeiensis* ($P = 0.0402$) and *M. viridis* ($P < 0.0001$; Table 6). *Mesocyclops pehpeiensis* killed more *Ae. albopictus* than did *M. viridis,* which in turn killed more *Ae. albopictus* than did *M. distinctus* ($P < 0.0001$; Table 6). When *Cx. tritaeniorhynchus* was exposed to copepods, no significant difference was found in number of larvae killed between the copepod species ($P = 0.5334$; Table 6). When *An. minimus* was exposed, *M. distinctus* and *M. viridis* killed similar numbers of larvae ($P = 0.9997$). Their predation on this mosquito was higher than that of *M. pehpeiensis* ($P = 0.0041$; Table 6).

DISCUSSION

Collection and systematics

Macrocyclops distinctus, M. viridis, and *M. pehpeiensis* were collected from rice fields in Nagasaki, Kyushu Island, Japan, where they are common during the early summer. The 2 latter species were more abundant in our samples and were easier to cultivate. The 1st species was very rare and was recorded only from Yamagata Prefecture in Japan, although it is widespread throughout the world (Guo 2000). The 2nd species has been recorded from various localities in Japan but not in Kyushu (Guo 2000). The 3rd species formerly was identified as *Mesocyclops leuckarti.* It is rare, and is found in Europe and Central Asia, but not in East Asia. This species was recorded as *Mesocyclops ruttneri* from Miyazaki Prefecture (Hueda et al. 1997). Recently, Guo (2000) reidentified *M. pehpeiensis* and concluded that *M. ruttneri* is a synonym of *M. pehpeiensis.*

Development and sexual maturation

Mate limitation has been shown to be unimportant for cyclopoid copepods (Smyly 1970, Whitehouse and Lewis 1973, Wyngaard and Chinnapa 1982), except when male densities are low (Watras and Haney 1980). Williamson and Butler (1987), when studying *Diaptomus pallidus* (a copepod related to those studied here), found no egg sac–carrying females in the absence of males and determined that high densities of males were associated with high mating success. In the present study, all 3 species produced a 1st clutch, indicating that at least 1 mating event occurred in each case. The shortest period for 1st reproduction that was recorded for *M. pehpeiensis* is most likely because it has a larger number of eggs. Regardless of egg and larval mortality, this species is likely to have more offspring compared to both *M. distinctus* and *M. viridis.* In this study, progenies were mixed, another mechanism that could increase mating chances in *M. pehpeiensis.* This may increase population size and thus allow higher encounter rates between the both sexes in this species.

Fecundity and longevity

The term reproduction in copepods has been used differently by various investigators. Hopkins (1977) defined reproduction as clutch size, whereas Hopp et al. (1997) considered it as the cumulative number of clutches produced in adult life. Environmental factors have been shown to influence reproduction by affecting either clutch size or the frequency with which clutches are produced (Williamson and Butler 1987). In our study, we found that the small *M. pehpeiensis* was more productive in term of absolute number of eggs per clutch, whereas in the long term, the larger species were more productive in all treatments, including when

Table 3. Mean (± SE) longevity (in days) of various copepod species under different nutritional conditions.[1]

Species	Starvation		Mosquito larvae		*Paramecium*	
	Mean	Range	Mean	Range	Mean	Range
Macrocyclops distinctus	29.1 ± 2.0 Aa	25–38	67.8 ± 6.2 Ba	39–84	53.0 ± 5.6 Ba	40–72
Megacyclops viridis	46.7 ± 2.5 Ab	42–64	78.6 ± 4.7 Ba	49–93	71.8 ± 11.6 Ba	33–120
Mesocyclops pehpeiensis	21.2 ± 0.3 Ac	20–22	23.5 ± 0.9 Ab	21–27	34.3 ± 1.0 Ba	31–37

[1] By analysis of variance, values in the same column with the same lowercase letter do not show a significant difference ($P > 0.05$). Those in the same row with the same capital letter do not show a significant difference ($P > 0.05$).

Table 4.　Mean (± SE) number of clutches produced by various copepod species under different nutritional conditions.[1]

Species	Starvation		Mosquito larvae		*Paramecium*	
	Mean	Range	Mean	Range	Mean	Range
Macrocyclops distinctus	1.5 ± 0.2 Aa	1–2	13.1 ± 2.2 Ba	4–19	8.6 ± 0.6 Ba	7–11
Megacyclops viridis	1.4 ± 0.2 Aa	1–2	17.0 ± 1.4 Ba	9–23	14.7 ± 3.6 Ba	3–28
Mesocyclops pehpeiensis	1.0 ± 0.0 Aa	0–1	4.50 ± 0.2 Bb	4–5	8.6 ± 0.5 Ca	6–10

[1] By analysis of variance, values in the same column with the same lowercase letter do not show a significant difference ($P > 0.05$). Those in the same row with the same capital letter do not show a significant difference ($P > 0.05$).

there was less productivity under starvation conditions. Clearly, body size and larval feeding history are likely to affect egg production. Possibly, *M. viridis* and *M. distinctus,* which are larger that *M. pehpeiensis,* store more nutrients for reproduction because evidence exists that small adult female copepods generally carry fewer eggs than do large individuals (Hopkins 1977).

Size has been considered as an important trait for screening a predator copepod because larger species are better predators (Fryer 1957, Marten et al. 1994). Therefore, if size is associated with a small clutch size, as is the case with *M. distinctus,* the potential for population increase may be poor. The lower presence of *M. distinctus* compared *M. pehpeiensis* and *M. viridis* in our samples in April 2000 and 2001, and the difficulties in cultivating *M. distinctus* in the laboratory, seem to confirm the poor population growth potential of this species (Dieng, unpublished data).

The females tested here produced fewer egg sacs when unfed and lived for a shorter period than those fed with either protozoans or mosquito larvae. This suggests that egg production depends on food type and quantity, as already has been demonstrated in other copepods (Hutchinson 1951, Checkley 1980, Hansen and Santer 1995, Hopp et al. 1997). Such a loss of reproductive potential because of food has been well studied in copepods. Marshall and Orr (1955) postulated that under unfavorable conditions, copepod females could delay egg laying or resorb egg material into the body. Corkett and McLaren (1969) reported that after a period of starvation, copepod females lose their ability to reproduce. Gilbert and Williamson (1983) indicated that scarcity of food retards oocyte pro-

duction and increases the proportion of females that do not bear eggs in copepod populations.

Mesocyclops pehpeiensis did not reproduce at all in the absence of food, whereas *M. distinctus* and *M. viridis* did reproduce. In addition, *M. pehpeiensis* had the same longevity whether unfed or reared with food. This demonstrates the high resistance to starvation in this species. However, resistance to starvation was much higher in *M. viridis* and *M. distinctus*; this is likely to be related to their ability to accumulate more energetic reserves and nutrients compared to the small *M. pehpeiensis.*

In these experiments, the females were kept without males but they produced eggs when food was available. This shows an ability of female copepods to store sperm and confirms previous results that argued that cyclopoid copepods do not need to remate to fertilize their eggs (Gilbert and Williamson 1983, Williams and Butler 1987, Maier 1992).

Predation on mosquitoes

All 3 species were observed to feed on the different mosquito larvae, with *M. distinctus* and *M. viridis* killing fewer *Ae. albopictus* than *M. pehpeiensis,* which, however, killed fewer *An. minimus.* According to Marten et al. (1994), a good copepod predator should kill more than 20 mosquito larvae daily. Thus, all 3 species are effective predators on *Ae. albopictus,* but only *M. distintus* and *M. viridis* should be considered good predators on *An. minimus.* Based on the performances of *Mesocyclops longisetus, Macrocyclops albidus, Megacyclops latipes,* and *Acanthocyclops vernalis* against *Culex quinquefasciatus* Say (Marten et al. 1994, Marten et al. 2000), the 3 species in the present study should be considered to be effective predators on *Cx. tritaeniorhynchus.*

Differences clearly existed between the preferred prey of the different species, which are likely to be due to both predator and prey characteristics. We studied 3 copepod genera and 3 mosquito genera with different morphological features, as well as different behaviors. Copepods are capable of judging prey speed (Kerfoot 1978) and attack only moving prey (Williamson 1981, DeMott and Watson 1991), indicating that their ability to detect prey depends on their activity but also on the prey char-

Table 5.　Mean (± SE) interclutch period (in days) of various copepod species fed with *Paramecium* infusion.[1]

Species	Mean	Number of clutches pooled
Macrocyclops distinctus	2.54 ± 1.6 a	46
Megacyclops viridis	2.88 ± 1.4 a	95
Mesocyclops pehpeiensis	2.04 ± 1.3 b	47

[1] By analysis of variance, values in the same column with the same letter do not show a significant difference ($P > 0.05$).

Table 6. Mean (± SE) numbers of 1st-stage larvae of various mosquito species found dead in containers without copepods (controls) and in containers with copepods.[1]

Copepod species	Aedes albopictus	Culex tritaeniorhynchus	Anopheles minimus
Macrocyclops distinctus	20.8 ± 1.4 Aa	18.1 ± 1.5 Aa	23.2 ± 1.9 Aa
Megacyclops viridis	27.3 ± 1.7 Ab	20.6 ± 1.6 Aa	23.1 ± 2.1 Aa
Mesocyclops pehpeiensis	34.9 ± 1.7 Ac	21.0 ± 2.7 Aa	14.8 ± 1.7 Ab
Control (no copepod)	0.94 ± 0.2 d	1.6 ± 0.4 b	9.6 ± 0.8 b

[1] By analysis of variance, values in the same column and with the same lowercase letter do not show a significant difference ($P > 0.05$). Those in the same row and with the same capital letter do not show a significant difference ($P > 0.05$). Lowercase letters are for the comparisons between control and treated containers, whereas capital letters are for the comparisons between copepod species.

acteristics (Kerfoot 1978). *Mesocyclops* sp. have been reported to have a high activity level with a average swimming speed of 1.0–1.5 mm/sec (Williamson 1981). Laboratory observations showed that *M. pehpeiensis* is more active than *M. viridis*, whereas *M. distinctus* is a less powerful swimmer (Dieng, unpublished data).

Larval *Ae. albopictus* were the most vulnerable to copepod predation, especially by *M. pehpeiensis*. Analysis of larval movement with high-speed photography has shown that *Aedes* species are very active (Natchigall 1965). This behavior may increase the amount of water disturbance and hence the signal to the attacking copepods. In a related study, Sih (1986) showed that when a single predatory *Notonecta* was present, larval *Culex pipiens* (L.) reduced their movement by 79.5% and their occupancy of the center by 85.1% (the corresponding reductions for *Aedes aegypti* (L.), which is related to *Ae. albopictus,* were 15.5% and 18.3%, respectively). *Culex pilosus* (Dyar and Knab), another species related to *Cx. tritaeniorhynchus,* moves infrequently (Strickman 1989). Low motility may reduce predation by minimizing detectability and this factor may explain why *Aedes* was the most vulnerable in these studies. The inefficiency against *Cx. tritaeniorhynchus* also could be due to the bristles on larval *Culex,* which may increase the apparent size of the larvae and therefore prevent their consumption (Marten et al. 1994). Low locomotion and surface-dwelling behaviors of *Anopheles* sp. (Jones 1954, Strickman 1989) may minimize encounter frequency with copepods, aiding greatly to their escape efficiency and reducing the efficacy of copepods as biocontrol agents on these species.

This work suggests the importance of an ecological approach to the study of potential biological control agents, especially study of their reproductive potential, a key factor for survival in prey habitats.

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