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How Does the Ambush Predatory Copepod *Megacyclops formosanus* (Harada, 1931) Capture Mosquito Larvae of *Aedes aegypti*?

Amit Kant Awasthi[1], Cheng-Han Wu[1], Kun-Hsien Tsai[2], Chwan-Chuen King[2], and Jiang-Shiou Hwang[1,*]

[1]*Institute of Marine Biology, National Taiwan Ocean University, Keelung 202, Taiwan*
[2]*Institute of Epidemiology, National Taiwan University, Taipei 106, Taiwan*

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Amit Kant Awasthi, Cheng-Han Wu, Kun-Hsien Tsai, Chwan-Chuen King, and Jiang-Shiou Hwang (2012) How does the ambush predatory copepod *Megacyclops formosanus* (Harada, 1931) capture mosquito larvae of *Aedes aegypti*? *Zoological Studies* **51**(7): 927-936. The purpose of this study was to understand the mechanisms through which an ambush predatory copepod, *Megacyclops formosanus* (Harada, 1931), captures mosquito larvae of *Aedes aegypti*. Fast-cam filming was used to study the predation mechanism of the ambush predator, *M. formosanus*, on *Ae. aegypti* mosquito larvae. Our study indicated that *M. formosanus* demonstrated 2 intermediate steps: aiming and stalking. Currently, intermediate predation steps are either ignored or not described for predatory copepods. The copepod's aiming/stalking distance varied at about 4-8 body lengths, whereas the attack distance was shorter than the aiming distance. The stalking speed was significantly slower than the attack speed. Copepods preferred a cone-shaped area in front of the 1st antenna for attack compared to behind the antenna. In conclusion, both intermediate steps, aiming and stalking, enhanced the predatory success of an ambush predatory copepod by targeting prey for a sudden attack.
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Key words: Aiming, Stalking, Ambush predatory copepod, Mosquito larvae, Predation mechanism.

Predator-prey interactions are frequently divided into 4 sequential events: encounter, attack, capture, and ingestion (Gerritsen and Strickler 1977, Drenner et al. 1978, Mahjoub et al. 2011a), and a successful interaction is defined as an interaction that results in a kill or ingestion by the predator (Gerritsen and Strickler 1977). Similar to other predators, the interactive behavior of predatory copepods is also separated into the following sequences: swimming, encounter, attack, capture, and ingestion (Kerfoot 1978). Predation is the main source of prey mortality, in which the goal of the predator is to maximize the energy gain and minimize the handling time of its potential prey. In contrast, prey must develop strategies to minimize mortality resulting from predation (Lima and Dill 1990, McNamara and Houston 1992, Hwang et al. 2009). Behavioral studies of predatory copepods revealed that behavioral and morphological characteristics of copepods and their prey have a considerable effect on outcomes of predation and thus, the zooplankton community structure (Kerfoot 1978, Williamson 1983 1986 1987, Chang and Hanazato 2003 2005, Hwang et al. 2009). Outcomes of predator-prey interactions commonly depend on predator and prey swimming behavior, jumping behavior, size, and palatability (Williamson 1983 1986, Kerfoot and Sih 1987, Landry and Fagerness 1988, Lee et al. 2010, Vandromme et al. 2010, Chang et al. 2011, Hwang and Martens 2011, Mahjoub et al. 2011b, Dhanker et al. 2012, Kumar et al. 2012). These characteristics affect

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*To whom correspondence and reprint requests should be addressed. Tel: 886-935289642. Fax: 886-2-24629464.
E-mail:Jshwang@mail.ntou.edu.tw

the probability of a prey being attacked and ingested by a predator (Kerfoot 1978, Stemberger 1985, Chang and Hanazato 2003, Kumar and Rao 2003). Predators must adjust according to their requirements (for example, mating), and must also use optimal strategies for capturing prey, because each prey has behavioral, structural, and anatomical differences. According to optimal foraging theory, each predator must develop its own attack and capture mechanisms to maximize energy gains (Lima and Dill 1990, McNamara and Houston 1992).

Cyclopoid copepods are crucial invertebrate predators in zooplankton communities, and are frequently present in lakes, drains, ponds, and reservoirs (Kerfoot 1978, Williamson 1983, Chang and Hanazato 2003, Kumar and Hwang 2006). Copepods are referred to as predators of several zooplankton communities, whereas rotifers and cladocerans are in a central position (Williamson 1983 1986, Chang and Hanazato 2003, Lapesa et al. 2004), and they are also widely used for mosquito control because of their predation ability (Kumar and Hwang 2006, Marten and Reid 2007, Murugan et al. 2011). Copepod feeding strategies are characteristically divided into 3 classes, including ambush feeders, cruising feeders, and suspension feeders (Gismervik et al. 1996, Kiørboe et al. 2009). Active cruising generates feeding currents with the help of feeding appendages, and prey are captured in these feeding currents (Strickler 1982, Flood 1991, Hwang and Strickler 2001), whereas passive ambush feeders capture prey by surprise attack (Feigenbaum and Reeve 1977, Jonsson and Tiselius 1990, Svensen and Kiørboe 2000). Ambush predators generally use mechanical sensory cues, encounter tactics such as “sit and wait,” and strike tactics, such as grasping. Copepods perceive their prey by mechanoreception and chemoreception and maneuver captured prey before ingesting it (Hwang and Strickler 2001, Jakobsen et al. 2006, Jiang and Paffenhöffer 2008). The most likely sensory structures involved in the remote detection of chemical and hydrodynamic stimuli are setae of the antennules (1st antennae) and mouthparts (Strickler and Bal 1973, Gill and Crisp 1985, Price and Paffenhöffer 1985, Hwang et al. 1994, Hwang and Strickler 2001). Because copepods numerically dominate the pelagic realm of the oceans, they must be capable of sophisticated feeding or predation strategies. Although ambush predation requires mechanosensory precision to conduct a sudden attack on prey (Kerfoot 1978, Greene 1983), ambush predation is highly successful in copepods in terms of abundance (Humes 1994, Kiørboe 2011). Each feeding mode produces various hydrodynamic disturbances in the ambient water, which cause various exposures to predators. Ambush feeding is increasingly risky for larger copepods (Kiørboe et al. 2009 2010a b). However, for small ambush feeding zooplankton, lower predation risks were suggested by optimal foraging models (Visser 2001 2007, Kiørboe et al. 2009).

Megacyclops formosanus (Harada, 1931) was used as a predator and *Aeedes aegypti* (L) mosquito larvae were used as prey to address the following questions: what types of strategic differences were exhibited by *M. formosanus* in predation sequences from previous copepod studies?; and which was the most decisive and flexible step by *M. formosanus* during predation? In addition to these questions, we attempted to determine the most successful site and strategy among several successful predation events for *M. formosanus*.

MATERIALS AND METHODS

Predator and prey

The cyclopoid copepod *Megacyclops formosanus* was collected from a pond (25°8' 36.72"N. 121°46'54.76"E, Keelung, Taiwan) with a 0.5-m-diameter, 153-μm-mesh plankton net. The copepod colony was started by inoculating 10 gravid female copepods into a rectangular glass aquarium filled with 3 L of culture medium consisting of ciliate species, rotifer species, and the alga *Chlorella vulgaris* in dechlorinated tap water. Copepods were reared at a temperature of 27 ± 2°C, pH 7, and a photoperiod of 12:12 h in an incubator. Copepods were fed mosquito larvae for 3 d prior to the experiment and then starved for 24 h prior to the experiment.

Eggs of *Ae. aegypti* strains were obtained from the Institute of Epidemiology, National Taiwan University, Taipei, Taiwan. Eggs were processed to hatching, and 0-12-h-old mosquito larvae were used for the experiment. Larvae were not fed prior to the experiment, and after completing the experiment, all *Ae. aegypti* larvae were fed to fish to prevent any expansion of disease vectors.

Video filming

A groove slide chamber was placed on a platform of an Olympus stereo zoom microscope (model SZX 9, manufactured in Japan). After placing the groove slide on the microscope, an individual *M. formosanus* with 300 μl of dechlorinated, autoclaved, filtered tap water was transferred to the groove slide. After 1 min of acclimatization by the copepod, an individual 0-12-h-old *Ae. aegypti* mosquito larva was also transferred onto the slide as prey. Recordings were conducted using an Olympus microscope with an attached Photron Fast Cam Ultima 1024 (model 500 Monchrome, made in Japan). The video optical setup and technology were similar to those described by Strickler and Hwang (1999) and Dahms and Hwang (2010). Fast-cam video recordings were conducted at a frame rate of either 60 or 125 frames/s according to the requirement of the experiment with a resolution of 1024 × 1024 pixels. Stepwise predation sequences of an ambush predatory copepod were recorded at a temperature of 27°C with the fast-cam with a storage memory of 1536 frames.

Predation steps for an ambush predatory copepod were defined as follows. Aiming: After pursuit, the copepod “sits and waits” for the prey to reach a suitable position and time to begin stalking it. Stalking: Similar to ambush mammalian predators, cyclopoids also performed stalking during predation. Stalking in a panther is described the “slow and quiet” movements toward the prey to kill, catch, or harm. In contrast, a copepod cannot restrict itself to slow movements because of its fast jumping movements; however, it exhibited a propensity to hide when moving closer to the prey for attack after aiming. Attack: An attack involved any movement of the copepod or physical contact produced by jumping movements of the predator toward the prey or grasping movements of the feeding appendages. Capture: Capture was defined as grasping the prey by the mouthparts of the predator. Ingestion: Ingestion consisted of disappearance of the prey within the feeding chamber of the copepod; ingestion was considered the end of a predation sequence, when the copepod resumed swimming. A schematic diagram is shown in figure 1.

Kinematic description of *Megacyclops* attacks on mosquito larvae

Attacks that revealed maximal descriptions of the predation mechanism were extracted and thoroughly analyzed using manual tracking software TrackIt (Strickler and Hwang 1999). Images were digitized frame by frame, and digitized images were tracked from the position of the copepod (tip of the head) by manual tracking (Vandromme et al. 2010, Wu et al. 2010).

Aiming/stalking and attack distances

The aiming/stalking distance was defined as the distance between the copepod and prey when the copepod “sits and waits” (aims for prey) for a suitable time to attack the prey. Similarly, the place from which the copepod jumped on the prey, without stopping, was considered the attack distance.

The distance, d (mm), traveled between 2 successive video frames was computed from the x and y coordinates as follows:

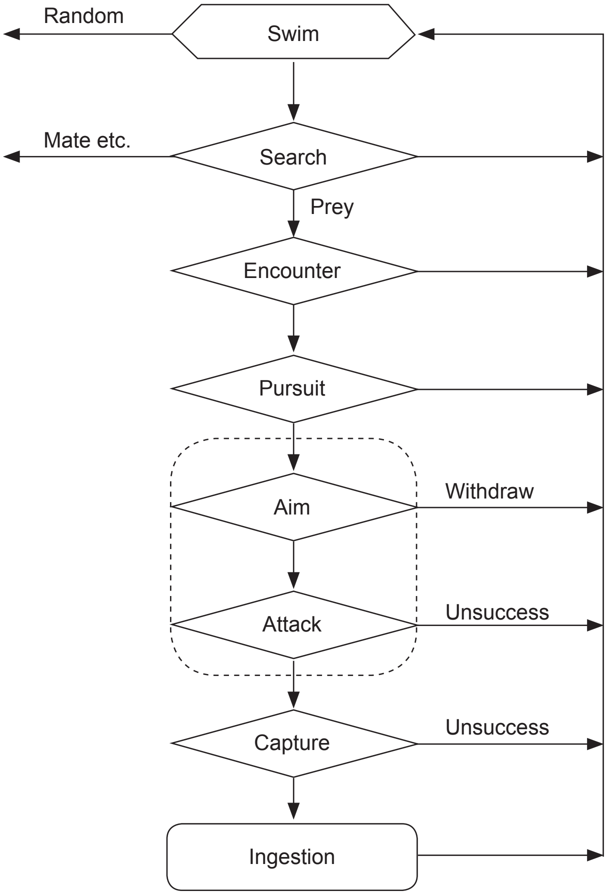

Fig. 1. Flow chart of predation steps shown by an ambush predator *Megacyclops formosanus* during predation. Predation sequences shown in the dotted box were stressed during the study.

$$d = [(x_t - x_{t+1})^2 + (y_t - y_{t+1})^2]^{1/2}; \quad (1)$$

where (x_t, y_t) and (x_{t+1}, y_{t+1}) are the positions of a copepod's head at times t and $t + 1$, respectively.

Stalking speed and attack speed

Stalking speed is when the copepod aimed for a prey and began to move closer toward the prey. After stalking, copepods attempted to move closer to the prey, and when they found a suitable location and time for attack, they suddenly jumped and captured the prey. The speed of copepod jumping on a prey was defined as the attack speed. The speed, v (mm/s), was subsequently estimated as follows:

$$v = d \cdot f; \quad (2)$$

where, d is the distance covered and f is the filming rate of the camera, that is, $f = 60$ or 125 frames/s.

Angle of attack and preferred attack field

The angle of attack was the angle from which copepod frequently attacked the prey. It was defined from the middle of the anterior-posterior body axis of the predator and the site on the mosquito larvae body at which the predator attacked. The 1st frame before the attack was used to compute the angles. All computations regarding speeds, attacks, and angles were calculated from the copepod prosome (tip of head) region.

RESULTS

This study of the ambush predatory copepod *Megacyclops formosanus* revealed that in addition to the 4 key steps (encounter, attack, capture, and ingestion), 2 intermediary steps were also necessary for this ambush predator (Fig. 1). The fast-cam study revealed that these 2 intermediate steps of aiming and stalking were essential for copepod prey-predator interactions (Figs. 1, 2A, B). Figure 2 shows the entire predation sequence that was recorded for an ambush predatory copepod. Aiming is shown in figure 2A (frame 1 at 0.017 s), and after aiming, the copepod began slowly

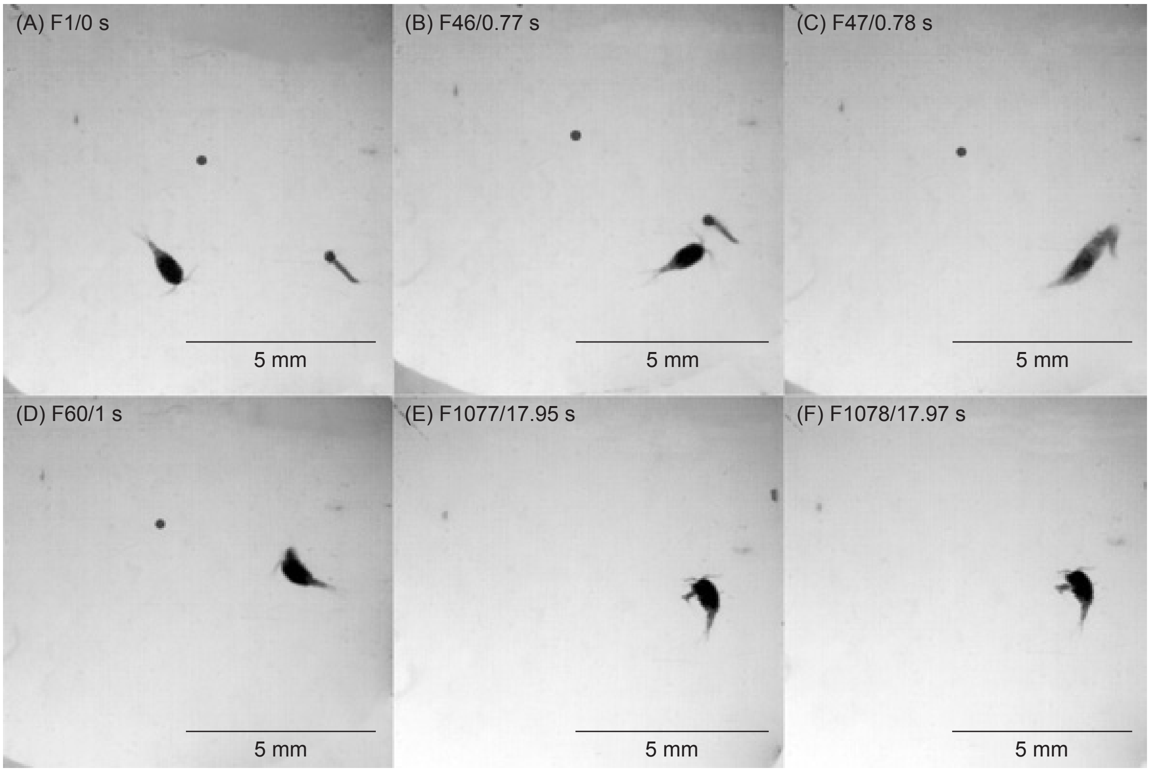

Fig. 2. Predation sequences showing the step-by-step predation mechanism of an ambush copepod predator, *Megacyclops formosanus*, preying on 0-12-h-old *Aedes aegypti* larvae recorded by high-speed video filming. Sequences represent the following: (A) aiming, (B) stalking, (C) attacking, (D) capturing, (E) ingesting, and (F) cutting into 2 pieces.

stalking its prey (Fig. 2B, frame 46 at 0.77 s). An attack occurred within milliseconds after stalking (Fig. 2C, frame 47 at 0.78 s). Copepod attacks resulted in either failure or success in capturing prey (Fig. 2D, frame 60 at 1 s). Successfully captured prey was subsequently directed toward ingestion (Fig. 2E, frame 1077 at 17.95 s). Subsequently, the copepod cut the prey into 2 pieces (Fig. 2F, frame 1078 at 17.97 s). If the copepod failed to capture the prey, it started over at the beginning. A copepod usually ingested almost the complete prey, except the head and thorax (HT) portions of a mosquito larva.

Figures 2A (frame 1 at 0.017 s) and 3A show aiming, in which the copepod "sits and waits" to attack a prey. The intermediary step of aiming is a mandatory phenomenon for predatory copepods, and it was consistently recorded in both successful and unsuccessful capture attempts during this fast-cam study. Aiming was demonstrated by the "sit and wait" strategy without producing any type of hydrodynamic disturbances in the water. The copepod moved closer to the prey before attacking it, and when it discovered a suitable "time and location" along with "best site and angle" for attack, it suddenly attacked the mosquito larva. After aiming, the copepod slowly stalked the prey and moved as close as possible without disturbing it. When the predator reached the prey, it decisively attacked the mosquito larva (Figs. 2, 3). After a successful capture, it moved to the next and final step of predation, which is ingestion of the prey by the predator.

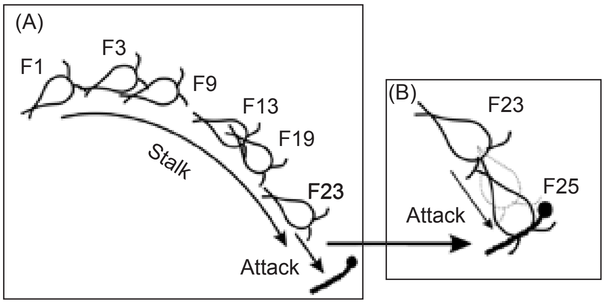

Fig. 3. (A) Pictographic sequences showing stalking after aiming (the copepod came closer to the prey within 0.38 s at F1-F23). (B) Represents an ambush predatory copepod attack on a mosquito larval prey within 0.03 s after reaching a logical site for an attack.

We measured aiming/stalking and attack distances for copepods. The critical difference between the aiming distance and attack distance was that the aiming distance was traveled by several swimming strokes, usually more than 5 strokes; however, the attack distance was usually covered by only 1 or 2 swimming strokes by the copepod. An independent *t*-test was used to compare between the aiming and attack distances and also for speeds, and significant results were obtained for both speeds and distances. The aiming/stalking distance varied considerably from 4 to 8 body lengths (6.36 ± 2.04 mm) of the copepod, and it was found to be significantly higher than the attack distance (1.50 ± 0.65 mm) ($p < 0.001$). The copepod stalking speed (14.63 ± 8.57 mm/s) was found to be significantly lower than the attack speed (31.10 ± 8.02 mm/s; $p < 0.001$) (Table 1).

The insect body is divided into 3 parts, and similarly, the mosquito larva body is also divided into 3 parts: the head, thorax, and abdomen. However, for our site-specific study, we segregated the larval body into 3 parts in a slightly different manner: the head and thorax (HT), abdomen (AB), and last body segment (LS) in which larval siphon is situated. We followed this body division plan because of the morphological and anatomical similarities and dissimilarities in these regions, and for convenience of analysis during the study. A fierce fight usually occurred when a copepod attempted to capture a prey by the HT region, which resulted in failure (Fig. 4). In total, 122 attacks were observed in this *M. formosanus* site-specific study, in which copepods attacked 3 distinct sites on mosquito larvae. The probability by Fisher's exact test was $p < 0.05$, which was less than the alpha level of significance of 0.05; hence, the null hypothesis was rejected, which indicated that "success and failure" depended on the site

Table 1. Copepod speeds and distances during stalking and attacking

	Stalking	*n*	Attacking	*n*
Speed (mm/s)	14.63 ± 8.57	12	31.10 ± 8.02*	22
Distance (mm)	6.36 ± 2.04	12	1.50 ± 0.65**	22

*Speed significantly differs ($p < 0.001$). **Distance significantly differs ($p < 0.001$).

of the attack. The AB was attacked the maximal number of times, and the number of attacks was 57 of 122 total observed attacks. The HT region was attacked by the copepod 38 times, which was the 2nd highest number of attacks, and the LS was the least attacked site at 27 times. The attack on the siphon (in the LS) endowed the copepod with the highest successful capture rate (63.0%), while the least successful capture rate (26.3%) was recorded for the HT site (Fig. 5).

Copepods reorient their body according to the prey, and typically prefer to attack in front of the 1st antenna in a cone-shaped direction. Copepods demonstrated their preference during attack, and their choice of attack occurred at 0° - 90° (Fig. 6). Copepods attacked prey at 0° - 45° 18 times out of 38 observed attacks, whereas the number of attacks was 14 at 45° - 90°. The total percentage of attacks for these 2 observed angles (0° - 45° and 45° - 90°) was 84.2%, and the remaining observed attacks occurred at 90° - 180°. Our observed attack frequency demonstrated that 15.8% of attacks by copepod occurred behind the antenna (Fig. 6).

DISCUSSION

Feeding is a complex process in hydrodynamic ecosystems (Mahjoub et al. 2012) because predators must maximize energy gain and prey must avoid death resulting from attacks by predators. The predation outcome characteristically depends upon the swimming speeds of both prey and predator, because the swimming speed positively affects the encounter rate (Gerritsen and Strickler 1977). In addition to the swimming speed, prey swimming behavior also influences prey vulnerability (Kerfoot 1978, Landry and Fagerness 1988, Roche 1990). Ambush predatory copepods exhibit sophisticated behavior, passively wait for their prey, and perform quick surprise attacks by precision maneuvering during rapid jumping (Kerfoot 1978, Kiørboe et al. 2009). Sudden copepod attacks on their prey at high speed result in the highest success rate of predation without considerable conflict. Copepods predominantly use their mouth appendages to generate a feeding current (Strickler 1975, Koehl and Strickler 1981, Price et al. 1983, Van et al. 2003); however, they mostly exploit the strokes of

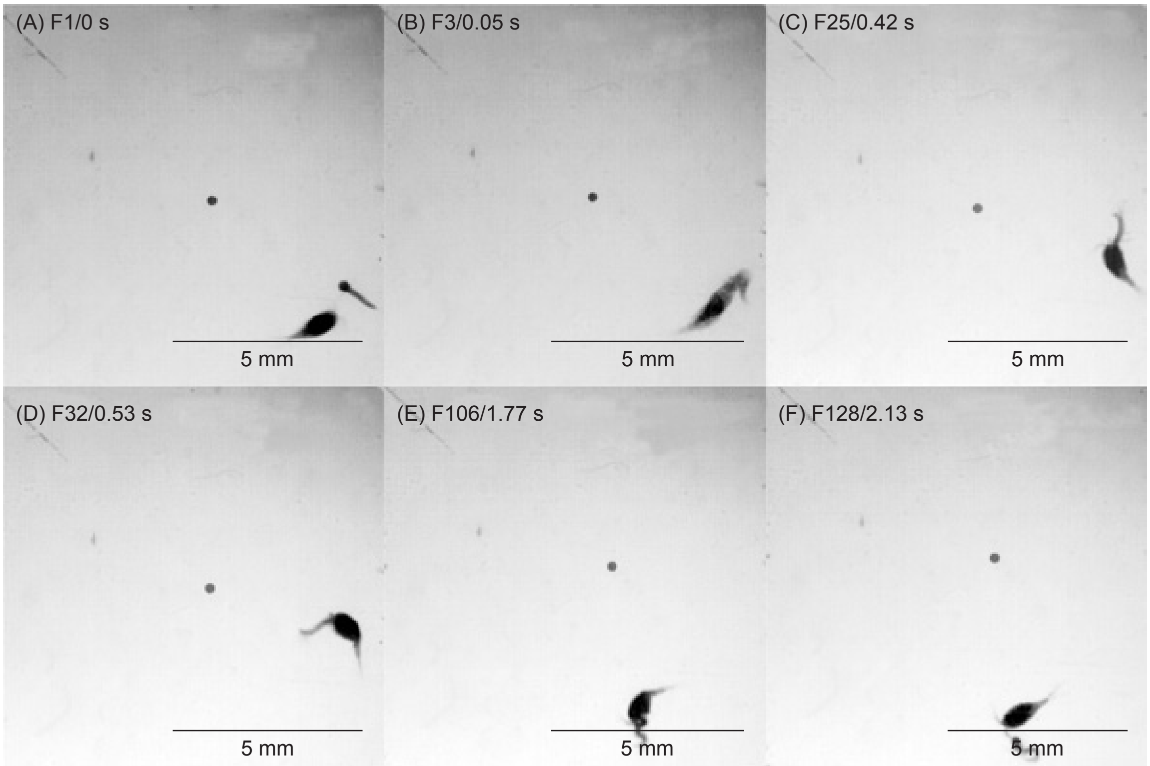

Fig. 4. Pictorial depiction of a fierce fight between a mosquito larva and a predatory copepod when the copepod was trying to capture the prey from the head and thorax (HT) region. The end result was failure by the copepod.

their antennae and swimming appendages to attain the high speed or to rapidly hop (jump) (Strickler 1975, Yen et al. 1992, Buskey et al. 2002, Van and Videler 2003). In copepods, the antennae are the main contributors to the net thrust force during hopping; therefore, they hydrodynamically facilitate thrust enhancement and drag reduction (Borazjani et al. 2010).

Copepods perform strong escape jumps at Reynolds numbers (Re) of > 100, which generate high hydrodynamic signals in ambient water (Yen and Strickler 1996, Van and Videler 2003). Although ambush copepods generate hydrodynamic signals in aquatic systems (Visser 2001 2007, Kiørboe et al. 2009), ambush feeding in copepods is highly successful in terms of both its omnipresence and high abundances (Feigenbaum and Reeve 1977, Humes 1994, Kiørboe 2011). Copepods must trade-off between particular feeding behaviors and the costs that they incur, including predation risks (Visser 2001 2007, Kiørboe et al. 2009). Slow stalking is a phenomenon that may reduce hydrodynamic signals in the water, which reduces perception by prey, as well as ensuring that the predator is out of sight. A reduced amount of hydrodynamic disturbance may assist a copepod in closely approaching its prey and ultimately achieving its goal of predation to capture the prey by not providing considerable hydrodynamic clues as to its presence. Reducing hydrodynamic traces by copepods in the water may be one of the possible reasons for the high success of ambush feeding by copepods.

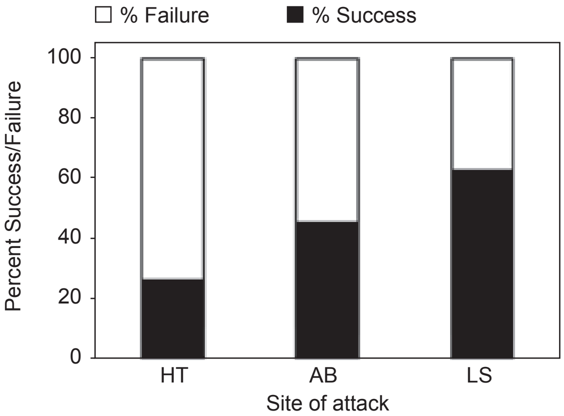

Fig. 5. Graph showing percentages of capture success and failure by the predatory copepod *Megacyclops formosanus* when it attacked 0-12-h-old *Aedes aegypti* larvae at 3 different places on the prey body: head and thorax (HT), abdomen (AB), and last segment (LS).

Copepods sense approaching prey from a distance, and therefore, they must precisely judge the approach angle and prey speed to reorient their bodies during an attack (Kerfoot 1978, Kerfoot and Sih 1987, Hwang and Strickler 2001, Lapesa et al. 2002). Copepods often vary handling responses according to their prey (Kerfoot 1978, Kerfoot and Sih 1987, Lapesa et al. 2002). Copepods aimed and stalked the prey before an attack. The aiming/stalking distance was consistently higher than the attack distance during the entire predation study. Copepods can attack from a single to several body lengths when they encounter numerous types of prey in a cone-shaped region at approximately 45° on either side of their bodies (Kerfoot 1978, Williamson 1986 1987, Lapesa et al. 2002). Aiming is a decisive stage in the copepod predation mechanism, in which the copepod determines the location of the attack and the manner, which ensures the success of the entire predation event to increase the capture efficiency and maximize the energy gain during predation. Ambush predators use mechanical sensory cues, encounter tactics, such as "sit and wait", and strike tactics, such as grasping, during the predation process (Strickler 1975, Greene 1983). Because ambush predation requires mechanosensory precision for sudden attacks (Gerritsen and Strickler 1977, Yen et al. 1992), aiming may enable them to achieve these goals. The sensory structures involved in detecting chemical and hydrodynamic stimuli are the setae of the antennules (1st antennae) and

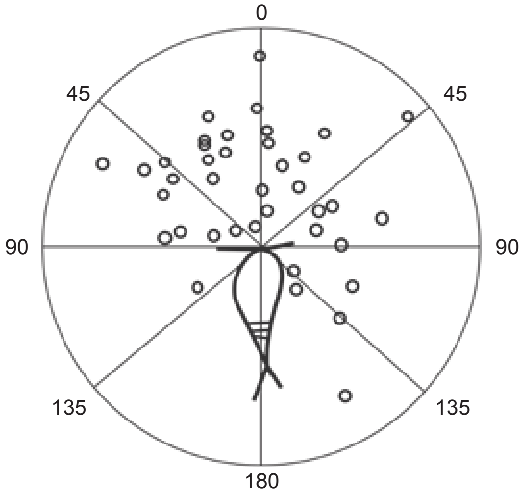

Fig. 6. Predatory copepod *M. formosanus* showing the attack preference in front of its 1st antenna in a conoid direction, at an angle of 0° - 45° and very little preference shown for behind the antenna.

the mouthparts of the copepod (Strickler and Bal 1973, Gill and Crisp 1985, Price and Paffenhöffer 1985, Hwang and Strickler 2001). The sensory structures, such as setae of the antennules and mouthparts, play a role in the remote detection of prey hydrodynamic stimuli in the water (Strickler and Bal 1973, Strickler 1975, Gill and Crisp 1985, Price and Paffenhöffer 1985, Buskey et al. 2002, Van and Videler 2003). With the help of sensory structures, the intermediate strategy of aiming may provide the precision to maneuver the prey, and also helps them determine whether to "attack" or "abort" the entire predatory sequence and begin searching again.

Copepod attacks were frequently directed toward the front, in a cone-shaped region in front of the 1st antennae, with reorientations executed in small fractions of a second. A fast attack speed requires the assistance of the antennae and swimming appendages, whereas precision requires the sensory setae of the 1st antennae during an attack (Strickler and Bal 1973, Strickler 1975, Gill and Crisp 1985, Price and Paffenhöffer 1985, Buskey et al. 2002, Van and Videler 2003). The antennae of copepods facilitate both precision and high speed during an attack. Therefore, copepods exhibited a strong preference for the front of the 1st antenna for attacks. Lapesa et al. (2002) and Kerfoot (1978) reported similar preferences for the cyclopoid copepod attack angle (pouncing angle) when they predate on rotifers and cladoceran prey.

Prey selectivity is influenced by several prey attributes, such as the size, shape, palatability, and behavior, such as swimming, speed, and jumping (Kerfoot 1978, Stemberger 1985, Landry and Fagerness 1988, Kumar and Rao 2003, Dhanker et al. 2012, Kumar et al. 2012). Copepods adapt prey selectivity patterns, which lead to ingestion of the most profitable prey (Stemberger 1985, Kumar and Rao 2003). This predatory copepod study revealed a differential capture efficiency for the attack site, which was not addressed in the related literature. This is the 1st paper to report that capture success of copepods was considerably dependent on the site of attack on mosquito larvae. A specific attack site of the prey ensured a number of advantages to the copepod in terms of interactions with the prey. Highest success was achieved when a copepod attacked the LS, and the least success was attained when they attacked on the HT region of mosquito larvae. Schaper and Hernández (2006) suggested that once a cyclopoid had damaged the respiratory system of a mosquito larva, the prey would not survive. The differential success rate for the predator may be attributed to 2 reasons: first, the mosquito larval head region has more setae than other parts, and larvae have a head capsule and more chitin compared to other body parts; and second, the head part is usually slightly larger than the other parts (Bruce and Rattanarithiku 1973, Rueda 2004). Copepod attacks on the mosquito larval siphon provide them with the most vulnerable site of the prey because the mosquito larval respiratory system is situated in the LS. Another predation study on *Ae. aegypti* indicated that larvae were mainly damaged at the siphon; only 3 attacks to the head were observed (Schaper and Hernández 2006). Attacking the most vulnerable site may be similar to prey selectivity, in which the predator usually prefers prey that can be easily managed (Kerfoot 1978, Roche 1990, Chang and Hanazato 2003, Lapesa et al. 2002 2004, Hwang et al. 2009). Mosquito larvae increase flexing in the presence of a predator (Juliano and Reminger 1992, Brackenbury 2001). Copepods usually failed when attempting to capture mosquito larvae from the HT site because mosquito larvae fought ferociously by increasingly flexing their bodies (Fig. 4). High-frequency flexing provides protection against predators, because a highly active prey is always more difficult to manage. Culicidae larvae exercise the terminal segment of the abdomen as a paddle for swimming (Houlihan 1971, Brackenbury 2001). Copepods often vary handling responses according to their prey (Kerfoot 1978, Williamson 1983 1986, Lapesa et al. 2002). If the captured prey attempted to escape from a copepod grab, the copepod used all of its feeding appendages to form a loop to kill the captured mosquito larva (Figs. 2, 4). Looping around the prey may assist the copepod in holding the prey firmly and also ensures that the prey is grasped in an efficiently engaged manner. Similarly, a tilted looping body of the copepod was also reported in a *D. bicuspidatus odessanus* predation study (Lapesa et al. 2002). However, before ingestion, the copepod must kill the captured prey to complete the predation process. Looping also provides strength to exert greater pressure on prey for killing and ingestion.

The differential capture success for site-specific attacks on prey by an ambush predatory copepod revealed that the copepod may choose the most vulnerable site on mosquito larvae. Maximal copepod attacks on prey were in a cone-shape direction in front of the antennae, and looping around the prey indicated that predators have specific strategies to handle the prey to minimize confrontation. The intermediate steps, “aiming” and “stalking,” provide precision to copepods to conduct a sudden attack on the prey. Thus, for an ambush predatory copepod, the intermediate steps, “aiming” and “stalking,” play vital roles in enhancing predation success.

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