DIRECTIONALITY AND SWIMMING SPEEDS IN PREDATOR-PREY AND MALE-FEMALE INTERACTIONS OF *EUCHAETA RIMANA*, A SUBTROPICAL MARINE COPEPOD

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ABSTRACT

This examination showed how the sexual dichotomy in morphology and feeding was reflected in the swimming behavior of *Euchaeta rimana*. Nonrandom swimming was clearly exhibited by this copepod, and the evolutionary reasons for the behaviors involve the dual requirements of encountering food and mates. Mechanoreceptive females, with their enlarged feeding appendages and elongated antennal setae, must find prey to feed. Non-feeding males, with reduced mouthparts and antennal setules, must find females to inseminate before exhausting their lipid reserves which were accumulated during juvenile stages. Directional swimming by the female predatory copepod supports the predictions of models in which encounter rate was maximized by swimming orthogonally to their mates and their prey. The female swam horizontally in a turn-and-search pattern to intersect the male which swam vertically in a swim-up-and-sink pattern. Adult female copepods (~2.5 mm prosome length) generally swam smoothly and continuously at an average swimming speed of 7 mm·s⁻¹, with their antennae oriented into the flow not disturbed by their own movements. Besides mating, females also must find and capture prey. Analysis of swimming by one potential prey, *Acartia fossae*, showed that these smaller copepods darted up and stopped in various directions to counteract sinking due to gravity. This resulted in a strong vertical component to their directionality which increased the likelihood of encounter with the predatory copepod. The dart-and-stop swimming pattern of *Acartia fossae* may be an alternate mode of escape from a mechanoreceptive copepod, such as *Euchaeta*, which can not sense prey when they are not moving.

Predation is successful when the predator ingests its prey. The predator must recognize the other animal as a potential prey item, attack it, and capture the prey (Gerritsen and Strickler, 1977). Similarily, mating is successful when reproduction occurs. However, prior to these events, the animals must first encounter each other. Encounter probability estimates, predicted by Gerritsen and Strickler (1977), assume random swimming. They conclude that for animals moving in three-dimensional space, there are two optimal strategies: (1) cruising predators which prey upon slow moving animals and (2) ambush (non-moving) predators which prey upon fast cruising prey. For cruising predators, a modification of the model by Gerritsen (1980) to include swimming directions has allowed further predictions of interactions whereby planktonic organisms can maximize their encounter rates with their prey and mates and minimize crossing paths with their predators. Theoretically, cruising predators can maximize their encounter rates behaviorally by swimming orthogonal to the predominant direction of their prey or mate as Gerritsen (1980) found for a predatory freshwater cyclopoid copepod and its prey. By increasing the rate of encounter, progress through the sequence of events leading to successful predation and mating is permitted.

Analyses of swimming behavior of copepods by visual techniques show distinct patterns, primarily in response to the presence of prey. Changes are noted in looping frequency at high and low prey densities (Williamson, 1983), where looping apparently is an attempt to locate prey. Pause and burst patterns also vary with changes in food concentration where, in the presence of phytoplankton, the

marine copepod *Pseudocalanus minutus* exhibits a decrease in the average swim-ming speed and an increase in "pause" behavior (Buskey, 1984). Another marine copepod *Centropages typicus* spends less time in slow swimming and more time at rest as food concentration decreases (Cowles and Strickler, 1983). These results show that predator search patterns are modified in response to changes in prey concentrations; the response increases their chances for predator-prey interactions. Another interaction showed a highly evolved adaptation for repelling nocturnal grazers, where bioluminescent flashes from dinoflagellates increase the number of high speed bursts by copepods (Buskey, 1984).

In this study, I used a laser-illuminated videomonitoring system (Strickler, 1985) to study interactions of free-swimming copepods. I examined the swimming behaviors of the pelagic predatory copepod *Euchaeta rimana,* its conspecific mates and various species of copepod prey to determine whether directionality was exhibited which could influence the probability of encounter. *Euchaeta rimana* is a subtropical oceanic planktonic copepod. This pelagic copepod is a common member of the plankton of the North Pacific central gyre (McGowan and Walker, 1979). It is one of the larger members (~2.5-mm prosome length of adult female) of the copepod community and resides in the upper 100 m within the mixed layer (Hayward, 1980; Yen, unpubl.). Members of this genus are known to be carniv-orous (Båmstedt and Holt, 1978; Yen, 1985). In the subtropical waters surround-ing the Hawaiian island chain, adult females of this species are often found carrying eggs (Finn, 1983; Yen, pers. obs.). Survival by these reproductively active pelagic predators swimming in three-dimensional space in areas of low population abun-dance must be facilitated by maximizing encounter rate with both prey and mates. The goal of this investigation is to determine whether these animals exhibit a directionality that could improve their encounter rate.

METHODS

The oceanic copepods were collected using a 333-μm mesh, 1-m diameter net gently towed from 100 m to the surface 2 km outside Kaneohe Bay, Oahu, Hawaii, where depths are greater than 200 m and and open ocean copepods can be obtained. Live animals collected in the hauls were gently sorted into sea water and maintained at 20°C. The culture vessels were supplemented with a variety of small copepods (~500-μm prosome length) for food. These small copepods were collected using a 110-μm-mesh, 0.5-diameter net towed within Kaneohe Bay near Coconut Island where the Hawaii Institute of Marine Biology is located. Under these conditions, *E. rimana* can be easily maintained in the laboratory for at least one month or longer.

Within the first 2 weeks after collection, observations of the swimming behavior of the copepods were recorded on a laser-illuminated videomonitoring system developed by Strickler (1985) for fol-lowing free-swimming copepods. I did the behavioral observations at Strickler's laboratory, formerly at the University of Southern California. Prey and predatory copepods were transported from Hawaii to Los Angeles in thermally insulated containers. Animals arrived in excellent condition and were suitable for these videotaped observations. The basic system of laser photography is a modification of the Schleiren optical pathway as designed by Toepler (1866) in which an object forms a light image on a dark background. The light energy of 0.1 μW·cm⁻² had no effect on the swimming behavior of *E. rimana* since the copepod did not change its behavior in dim light or when exposed to the laser light. The speed of the videotapes was 30 frames·sec⁻¹. The activity of the copepods was recorded, in the dark, in a tank of the following dimensions: 12 × 12 × 15 cm (length × width × height). The tank was filled with 1 liter of glass-fiber filtered sea water. Ten to twenty *E. rimana* were placed in the tank with 20 to 40 small copepods added as prey. Prey were either collected in Kaneohe Bay, Oahu, with a 110-μm 0.5-m net and brought to Los Angeles or they were collected in a similar manner off Long Beach, California. To make sure the behavior was observed repeatedly, observations were made of several different individual copepods on different days. These copepods were selected from different net hauls taken five separate times between August 1986 through February 1987.

Directional swimming was characterized by the following motions: vertical (up and down) swimming (0° and 180°), horizontal (left and right) swimming (90° and 270°), up towards the right (45°), up towards the left (315°), down towards the right (135°), and down towards the left (225°). The percentage of time spent swimming horizontally and vertically was determined at the specified angles ±10°.
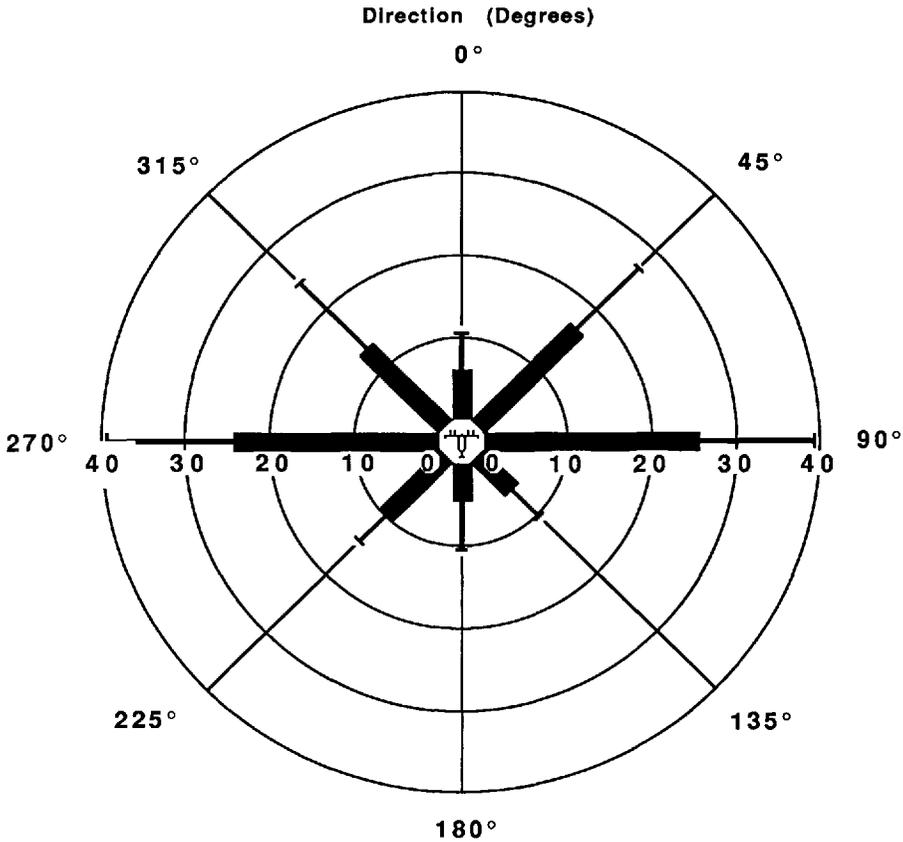
Figure 1. Directional swimming exhibited by adult *Euchaeta rimana* demonstrating a strong horizontal component. Six different females collected from 3 different dates were analyzed for at least 50 sec each for a total swimming time of 713 sec. The mean percent time spent swimming (±95% C.I.; N = 6) in each direction is shown.

Swimming directions in the range of 10° to 80° were pooled at 45°. All directions between 100° and 170° were pooled as 135°. All directions between 190° and 260° were pooled as 225°. All directions between 280° and 350° were pooled as 315°. The frequency and duration of the separate behavioral events as described above and including turns exhibited by swimming copepods were quantified and statistically analyzed using a computerized event recorder called the BEAST (Behavioral Events Acquisition and Analysis System; developed at Windward Technology by G. Losey, 1984). Each event was recorded by visually following the movements of the copepod and pressing buttons on the computer, where the number of times each button was pushed and the amount of time the button was pressed represented the frequency and duration of each event. Only copepods situated at least two body lengths (5 mm) away from the walls of the tank were analyzed. Length calibrations were accomplished by videotaping a millimeter ruler. Swimming speeds were computed as displacement over time relative to a non-moving object on the videotape. Swimming speeds were computed only from those copepods in good focus indicating that they were traveling parallel to the plane of view. Comparisons to swimming behavior in the absence of food or mates were not done.

RESULTS

Adult females of *Euchaeta rimana* exhibited a strong horizontal (90°, 270°) component to swimming (Fig. 1). Swimming at an average speed of 7.06 ± 0.35 mm·sec⁻¹ (95% C.I. are always presented; N = 42 for seven measurements taken from six individuals), the female copepod was oriented so that the paired setular
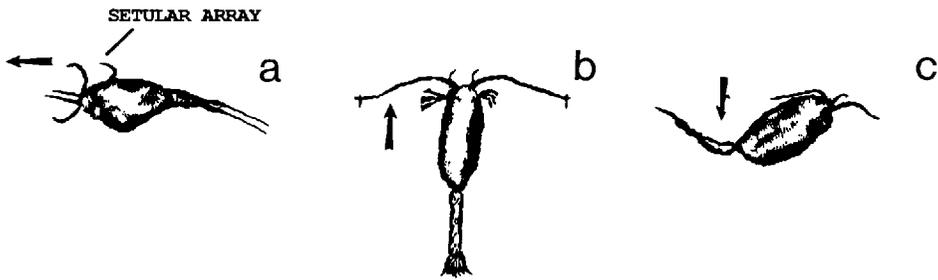
Figure 2.   Digitized images from videotapes of *Euchaeta rimana*. Arrow denotes direction of motion. (a) Adult female swimming. Note the orientation of setular array on first antennae into water not disturbed by self-generated hydrodynamic commotion. (b) Adult male swimming. Note orientation of slim body along the streamline movements of upwardly directed swimming. (c) Adult male sinking. Body orientation during sinking was with the ventral surface down and abdomen arched.

array projecting from the first antennae was the first section of the body to enter water not disturbed by the presence of the swimming copepod (Fig. 2a). Swimming was propelled by the beating of the second antennae. The copepod never glided on the momentum generated by swimming or jumping. If there was no appendage movement, the copepod immediately sank. The gentle cruising of the copepod was interrupted only briefly by the rapid turns which took less than 60 ms to execute. Frame-by-frame analysis of the turn indicated that the copepod used its swimming legs to propel itself through the turn. Simultaneously, the urosome was flexed down toward the body to create torque to direct the turn and the first antennae were folded down against the body. Immediately after completing the turn, the animal swam for less than 0.5 s with a slight downward component followed by horizontal swimming with a slight rise in the swim path. Turns, which occurred on the average every 2.6 ± 0.34 s (95% C.I., N = 180) in the 12 cm × 12 cm tank, may occur at a lower frequency in a larger vessel. However, the analyzed turns were performed at least two body lengths away from the walls of the tank.

Measurements of lunge speeds, where the predator attacked a moving copepod prey, showed that *E. rimana* could swim at speeds up to 142 mm·s^{-1} or 60 body lengths·s^{-1} for a 2.4 mm (prosome length) copepod. Acceleration cannot be observed using videotaped observations since the camera records at a speed of 30 frames·s^{-1} and often, the lunge occurred in less than two frames when the copepod went from its near-stationary position into a lunge followed by rapid deceleration.

Adult males of the copepod *E. rimana*, which lack the setular array on their first antennae, swam with a predominantly vertical (0°, 180°) component (Fig. 3). The males swam up with their long axis of the body aligned with the flow (Fig. 2b) at a speed of 7.5 ± 0.4 mm·s^{-1} (95% C.I., N = 11) and sank with their ventral surface down and urosome arched (Fig. 2c) at a speed of 5.0 ± 0.4 mm·s^{-1} (95% C.I., N = 11). Escape speeds can reach up to 360 mm·s^{-1} or 150 body lengths·s^{-1} for a 2.4 mm copepod. Upward swimming was accomplished by the beating of the second antennae. No motion of the mouthparts or swimming legs occurred during sinking. Even though males and females were filmed in the same tank, mating was not observed in the laboratory.

Acartia fossae (0.7 mm prosome length), a calanoid copepod and potential prey of *E. rimana*, was chosen for filming. Maximum feeding rates were measured on prey within this size range (Yen, unpubl.). To maintain their position, these prey exhibited upward swimming in various directions to counteract the downward
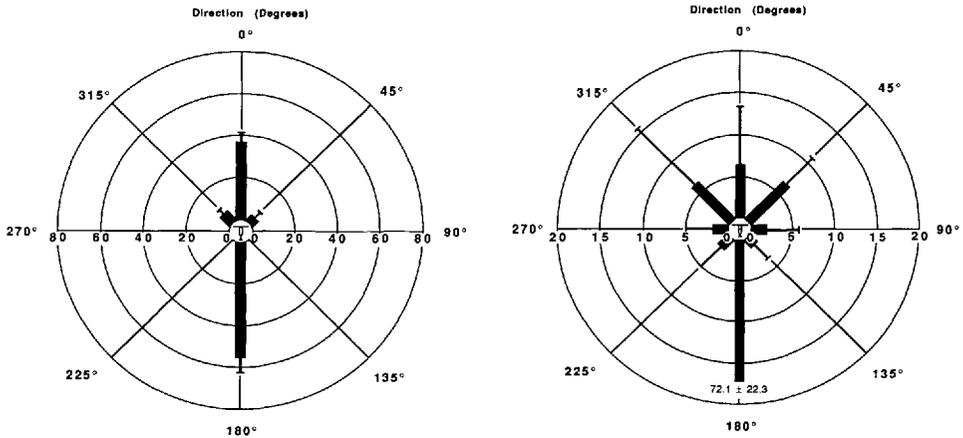
Figure 3. Directional swimming exhibited by adult make *Euchaeta rimana* demonstrating a strong vertical component. Seven different males collected from three different dates were analyzed for 20 to 130 sec each for a total swimming time of 465 sec. The mean percent time spent swimming (±95% C.I., N = 7) in each direction is shown.

Figure 4. Directional swimming exhibited by *Acartia fossae*. Four different copepods collected from three different dates were analyzed for at least 30 sec each for a total swimming time of 233 sec. The mean percent time spent swimming (±95% C.I.; N = 4) in each direction is shown. Value on 180° bar represents mean per cent time ±95% C.I.

component of sinking due to gravity (Fig. 4). This resulted in a predominant vertical component to their directional swimming. The average swimming speed for *A. fossae* is not reported since it swam intermittently, with rapid darts at speeds up to 87 mm·s⁻¹, followed by slow, almost imperceptible sinking lasting up to 2.5 s (Fig. 5).

Another copepod that frequently elicited attacks by *E. rimana* is *Corycaeus* sp., a small cyclopoid copepod. In the first sequence, a juvenile of this cyclopoid (0.35-mm prosome length) swam with a rhythmic motion, resting for 83 ± 31 ms (N = 22) followed by short jumps at speeds averaging 10 mm·s⁻¹ or 27.2 ± 5.0 body lengths·s⁻¹ (N = 23; Fig. 5). This "locomotive"-type activity propelled the copepod in one direction, usually upward. In another sequence (Fig. 6), the swimming activity of the predator, *E. rimana,* influenced that of its prey. The predator lunged for the prey at 43.5 mm·s⁻¹ or 17.4 body lengths·s⁻¹ for a 2.5 mm predator. The lunge motivated an escape by the prey at 64.5 mm·s⁻¹ or 107 body lengths/s for a 0.6 mm copepod. Slow swimming by both prey and predator was interrupted with a second lunge by the predator which caused the prey to dart 8 mm away within 100 msec at a speed of 129 mm·s⁻¹ or 215 body lengths·s⁻¹. This jump took the prey completely out of range of *E. rimana.*

DISCUSSION

Adult female copepods of the genus *Euchaeta* are tactile, nonvisual, not strongly chemosensitive copepods. They are size-selective carnivorous marine copepods that feed on active prey (Yen, 1982a; 1982b; 1983; 1985) as cruising predators (Greene and Landry, 1985). The female copepod feeds in the dark and shows little response to chemical stimuli (Yen, 1982a). It apparently uses an elaborate setular array on its first antennae to mechanoreceptively sense mobile prey (Yen and Nicoll, submitted[1]). Prior to capture, the predatory copepod must first en-
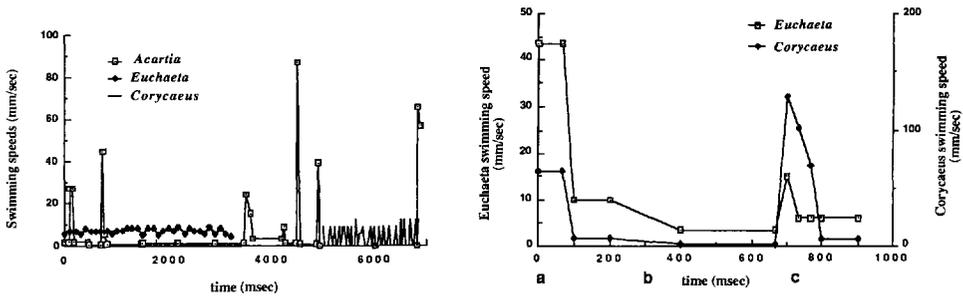
Figure 5. Variation in swimming speeds exhibited by three copepods: *Euchaeta rimana* (2.5 mm Prosome Length)—smooth continuous swimming at an average speed of 7 mm·sec^{-1}, *Acartia* (0.7 mm PL)—high speed darting (up to 90 mm·sec^{-1}) with 1–2 sec intervals of sinking, *Corycaeus* (0.35 mm PL)—rhythmic darting at 10 mm·sec^{-1} with short 83-msec intervals of no movement.

Figure 6. Swimming speeds of interacting prey (*Corycaeus*; 0.6 mm) and predator (*Euchaeta rimana*; 2.5 mm). a) Initial lunge by *E. rimana* at a speed of 43.5 mm·sec^{-1} made *Corycaeus*, which is 2.1 mm away (distance between tips of their prosomes), dart away at 64.5 mm·sec^{-1}, increasing the distance between the predator and prey to 3.5 mm. b) *Corycaeus* drifted slowly away at a speed of 1 mm·sec^{-1} while *E. rimana* continued to swim in its direction at a cautious speed of 3.5 mm·sec^{-1}. When *E. rimana* was 3.7 mm away from the cyclopoid copepod (with the antenna of the predator nearly touching the small copepod), *E. rimana* again lunged for the prey at a speed of 15 mm·sec^{-1}. This time, *Corycaeus* darted away at a speed of 129 mm·sec^{-1} so that within 100 msec, it was 8 mm away from the predator and had successfully evaded capture.

counter the prey. As predicted for cruising predators by Gerritsen (1980), *E. rimana* females swam in a way that maximized encounter with their mates and prey. The female swam horizontally in a turn-and-search pattern. Turns were brief since during the turn, the copepod is essentially "blind" because it is enveloped in the turbulence created by its own movements. During this time, a mechanosensitive copepod, such as *Euchaeta,* may not be able detect any hydrodynamic disturbance unless the magnitude of the disturbance is greater than that caused by the turn. This horizontal swimming improved the predator's chances to intercept the smaller prey copepod, *A. fossae,* which swam with a strong vertical bias. By swimming orthogonally to the prey, the predator can increase its encounter rate by up to 41%, assuming equal swimming speeds (Gerritsen, 1980). Since the swimming speeds often differed, the encounter advantage may be less than 41%.

For prey, the best strategy to avoid encounter with predators is to move slowly; however, prey animals also must encounter mates and their own food (Gerritsen and Strickler, 1977). One solution exhibited by the prey *Acartia* or *Corycaeus* was to combine high swimming bursts with intermittent pauses of slow sinking. During the akinetic sinking, mechanoreceptive detectors may be less able to detect prey due to the reduced amount of fluid deformations produced by the prey (Kerfoot et al., 1980). The slower the sinking and the smaller the body size, the more effective is this kind of crypsis. Slow sinking also allows the animal to scan the fluid for chemical or physical signals (Cowles and Strickler, 1983). Variable swimming speed is not a component of the encounter model which uses average speed. Computer simulations by R. Zaret (pers. comm.) suggest that encounter rates between a zooplankter and its neighbors increase as its motion becomes less continuous. Here, the average prey speed was similar to or less than that of the predator but instantaneously, prey intermittently exhibited much faster speeds.

[1] J. Yen and N. T. Nicoll. The structure of the first antennae of a carnivorous marine copepod *Euchaeta norvegica*; early detection by active prey using a mechanoreceptive detector. Mar. Biol. Submitted.

These high speed jumps allowed the prey to quickly displace themselves outside the capture/perceptive range of the predator.

Adult male *E. rimana* do not feed in the final adult stage (Yen, pers. obs.) and therefore do not need to encounter prey. In fact, during the final molt, the male is left with degenerated mouthparts and their first antennae lack the setular array that is so prominent on the female and juvenile copepods. The only role of the adult male copepod apparently is to find females and attach spermatophores. Since males can not feed, they must conserve energy to survive long enough on their lipid stores so that they can successfully mate. Vertical swimming became the primary swimming direction. According to Haury and Weihs (1976), discontinuous motion, like the hop-and-sink pattern, exhibited by the male copepods, is more energetically favorable. Besides the change in the morphology of the mouthparts and first antennae, the whole body form of the male copepod changes. The body form is much slimmer than the female shape which helps reduce drag so energy can be used for swimming and encountering females. Alignment of the body with the flow during the upward swimming should minimize resistance while sinking with the ventral surface down should increase the drag thus reducing the speed of sinking. The urosome was arched which may help maintain this posture or orientation during sinking. Vertical swimming, propelled by the second antennae, must be facilitated by these changes in body shape. Although the females and males of this species swim in different directions, they are both able to maintain their depth distribution; in this species, the adult female copepods do not exhibit a diel vertical migration (Ambler and Miller, 1987; Yen, pers. obs.). They remain in the upper stratum (100 m), where the males also are found, thus further increasing the likelihood of encounter between mates.

This examination showed how the sexual dichotomy in morphology and feeding was reflected in the swimming behavior of *E. rimana*. Nonrandom swimming was clearly exhibited by this copepod, and the evolutionary reasons for the behaviors involve the dual requirements of encountering food and mates. Mechanoreceptive females, with their enlarged feeding appendages and elongated antennal setae, must find prey to feed. Non-feeding males, with reduced mouthparts and antennal setules, must find females to inseminate before exhausting their lipid reserves which were accumulated during juvenile stages. Directional swimming by the female predatory copepod support the predictions of models in which encounter rate was maximized by swimming orthogonally to their mates and their prey. Prey must resort to other modes of escape, such as akinetic crypsis (Kerfoot et al., 1980), variations in shape such as streamlining to reduce hydrodynamic disturbances or protuberances which foil handling attempts, or high speed leaps which propel the prey outside the perceptive volume of the predator. Retraction of vulnerable swimming appendages also can make prey more difficult to grasp (Williamson, 1983). Future research should determine how the copepods are able to distinguish between prey, predators, and mates, and the mechanics and function of their sensory receptors.

LITERATURE CITED

Ambler, J. W. and C. B. Miller. 1987. Vertical habitat-partitioning by copepodites and adults of subtropical oceanic copepods. Mar. Biol. 94: 561–577.

Båmstedt, U. and M. R. Holt. 1978. Experimental studies on the deep water pelagic community of Korsfjorden, western Norway: prey-size preference and feeding of *Euchaeta norvegica* (Copepoda). Sarsia 63: 225–236.

Buskey, E. J. 1984. Swimming pattern as an indicator of the roles of copepod sensory systems in the recognition of food. Mar. Biol. 79: 165–175.

——— and E. Swift. 1983. Behavioral responses of the coastal copepod *Acartia hudsonica* (Pinhey) to simulated dinoflagellate bioluminescence. J. Exp. Mar. Biol. Ecol. 72: 43–58.

Cowles, T. J. and J. R. Strickler. 1983. Characterization of feeding activity patterns in the planktonic copepod *Centropages typicus* Krøyer under various food conditions. Limnol. Oceanogr. 28: 106–115.

Finn, J. A., Jr. 1983. Reproduction and feeding in the tropical, carnivorous copepod *Euchaeta rimana* Bradford. M.Sc. Univ. Hawaii. 55 pp.

Gerritsen, J. 1980. Adaptive responses for encounter problems. Pages 52–62 *in* W. C. Kerfoot, ed. Evolution and ecology of zooplankton communities. Univ. Press New England, Hanover.

——— and J. R. Strickler. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. J. Fish. Res. Bd. Can. 34: 73–82.

Greene, C. H. and M. R. Landry. 1985. Patterns of prey selection in the cruising calanoid predator *Euchaeta elongata*. Ecology 66: 1408–1416.

Haury, L. and D. Weihs. 1976. Energetically efficient swimming behavior of negatively buoyant zooplankton. Limnol. Oceanogr. 21: 797–803.

Hayward, T. 1980. Spatial and temporal feeding patterns of copepods from the North Pacific central gyre. Mar. Biol. 58: 295–309

Kerfoot, W. C., D. L. Kellogg and J. R. Strickler. 1980. Visual observations of live zooplankters: evasion, escape, and chemical defenses. Pages 10–27 *in* W. C. Kerfoot, ed. Evolution and ecology of zooplankton communities, Univ. Press New England, Hanover, New Hampshire.

McGowan, J. A. and P. W. Walker. 1979. Structure in the copepod community of the North Pacific central gyre. Ecol. Monogr. 49: 195–226.

Strickler, J. R. 1985. Feeding currents in calanoid copepods: two new hypotheses. Pages 459–485 *in* M. S. Laverack, ed. Physiological adaptations of marine animals. Symp. Soc. Exp. Biol. 89.

Toepler, A. 1866. Uber die Methode der Schlierenbeobachtung als mikroskopisches Hilfsmittel, nebst Bemerkungen zur Theorie der schiefen Beluechtung. Poggendorf's Ann. Phys. Chem. 127: 556 –580.

Williamson, C. E. 1983. Behavioral interactions between a cyclopoid copepod predator and its prey. J. Plankt. Res. 5: 701–711.

Yen, J. 1982a. Sources of variability in attack rates of *Euchaeta elongata* Esterly, a carnivorous marine copepod. J. Exp. Mar. Biol. Ecol. 63: 105–117.

———. 1982b. Predatory feeding ecology of *Euchaeta elongata* Esterly, a carnivorous marine copepod. Ph.D. Thesis, Univ. Washington, Seattle.

———. 1983. Effects of prey concentration, prey size, predator life stage, predator starvation and season on predation rates of the carnivorous marine copepod *Euchaeta elongata*. Mar. Biol. 75: 69–77.

———. 1985. Selective predation by the carnivorous marine copepod *Euchaeta elongata*: laboratory measurements of predation rates verified by field observations of temporal/spatial feeding patterns. Limnol. Oceanogr. 30: 577–597.

APPENDIX: DISCUSSION AFTER YEN

C. Greene: The temperate species of *Euchaeta* swims with a stronger vertical component to their directionality. The pattern is somewhat sinusoidal. Why do you think the subtropical species exhibits a strong horizontal component?

J. Yen: The temperate species undergoes an extensive diurnal migration with a

200 to 400 m difference in day vs. night depth, while the subtropical species remains within the mixed layer or above 100 m. Since the temperate species is such a strong vertical migrator, it may have this strong vertical component to its directional swimming to facilitate its migratory behavior. The subtropical species remains within the upper stratum. To maintain its horizontal position, it swims with a strong horizontal component.

D. Stearns: Did you always find that the prey began its escape behavior *after* the predator began its lunge, or did the prey detect the predator before the lunge?

J. Yen: My preliminary observations indicate that attacks by *Euchaeta* are elicited when prey, drawn towards the predator by currents generated with the second antennae, become aware of the predator and dart away to escape. Almost simultaneously with the dart, *Euchaeta* lunges at the escaping prey, so it is probably sensing fluid displacements within the prey's wake. However, the readiness of the lunge and the accuracy of the pounce suggest that *Euchaeta* may also have prior knowledge of the presence of prey in close proximity, perhaps due to oscillations of the prey's feeding appendages. The wake and the strength of this disturbance may have indicated that the prey was within strike distance, thus eliciting an attack.

J. Atema: This points out some important information that is lacking in most existing observations of zooplankton feeding. We need to know the true "fields" of mechanical and chemical signals, as well as the grazer's "perceptive volume."

J. Yen: I plan to look at the perceptive volume of *Euchaeta* using Rudi Strickler's new system. Since there are two perpendicular cameras, I can get the 3-D location of the predator and prey prior to attack. I want to see how the shape of the perceptive volume changes with prey type and the amount of hydrodynamic "noise" the prey makes.