

SETAL ARRAY ON THE FIRST ANTENNAE OF  
A CARNIVOROUS MARINE COPEPOD,  
*EUCHAETA NORVEGICA*

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ABSTRACT

A unique and elegant setular array on the first antenna of the adult female stage of the carnivorous marine copepod *Euchaeta norvegica* is described. The setae are aligned along 3 planes where the paired antennae cover one plane. The second plane is covered by elongate straight setae that project anteriorly at the proximal section of the antenna and posteriorly at the distal tip of the antenna. A pair of elongate curved setae on the seventh and eighth segments of the first antenna projects perpendicular to the plane of the antenna and perpendicular to the plane of the straight setae. These 2 curved setae flanked by 2 straight setae on segments 3 and 13 project equidistant in front of the antenna. They form a 4-point quadrangular setal arrangement on each antenna. The paired structure may be designed for the early detection and localization of objects moving in 3 dimensions in the copepod's immediate environment.

First antennae are important sensory structures on many copepods (Friedman and Strickler, 1975; Gill and Crisp, 1985; Haury *et al.*, 1980; Strickler and Bal, 1973). Haury *et al.* (1980) considered the setae of the first antennae as the most likely receptors involved with detection of fluid disturbances. Setae appear to be modified ciliary structures which function as mechanoreceptors, detecting gravitational and inertial forces transmitted by fluid mechanical means (Friedman, 1980; Markl, 1978; Strickler and Bal, 1973). Gill (1985) commented further that it is reasonable for the tips to be the most sensitive part of the antennae since they are farthest away from the body and therefore can detect stimuli with least interference from the movement of other limbs. Since the antennae and setae are on different scales, they would be expected to respond in different ways to different levels of fluid stimuli (Haury *et al.*, 1980). Furthermore, within each copepod taxon, differences in arrangement and size of setae and aesthetascs among the proximal, middle, and distal sectors of the first antennae suggest that these sectors receive different ranges as well as directionality of chemical and mechanical signals (Fleminger, 1985). To determine their function, we must first describe their morphology.

This is a morphological study of the first antennae of adult calanoid copepods of the genus *Euchaeta*. Species of *Euchaeta* are predators, employing enlarged maxillipeds to feed on crustacean prey (Lowndes, 1935;

Mullin, 1967; Båmstedt and Holt, 1978; Yen, 1985) as well as on fish larvae (Bailey and Yen, 1983; Yen, 1987). An examination of the predatory feeding ecology of 4 species of *Euchaeta* showed that they exhibit size selective predation, vertical migratory activity, and variations in body size (clutch size, lipid storage capabilities) in response to seasonal and latitudinal differences in food availability and environmental conditions (Yen, 1982a, b, 1983, 1985). These euchaetid copepods have been found to be important macroplanktonic carnivores and biomass dominants in many oceanic systems (subarctic: Båmstedt and Skjoldal, 1976; antarctic: Hopkins, 1985; temperate: Ohman *et al.*, 1983; Yen, 1985; subtropical: McGowan and Walker, 1979). Their prominence in the marine zooplankton community also depends, in part, on an acute sensory system.

In this study of *Euchaeta*, photographs of freely swimming copepods showed the natural orientation of an elegant array of setae projecting from their first antennae. The specific orientation of this paired array may enhance the copepod's ability to detect prey. We suggest that the array plays an important function as a mechanoreceptor of fluid displacements in close proximity to this predatory copepod.

MATERIALS AND METHODS

*Collection.*—Copepods of the subarctic species *Euchaeta norvegica* were collected with a 500- $\mu$ m mesh, 1-m diameter net gently towed obliquely from 175 m

to the surface in Loch Etive, Scotland, on board the RV *Calanus* of the the Scottish Marine Biological Association Laboratory in Oban, Scotland. Actively swimming adult females were separated from the plankton collection and placed in tanks of clean sea water. A variety of small copepods (approximately 1 mm in prosome length) consisting mainly of *Pseudocalanus* sp. was added to the tanks as food for the predators.

**Photography.**—To examine the morphology of the sensors, we took photographs of live specimens of the large subarctic *E. norvegica* (6 mm in prosome length), swimming in water. Photographs were taken by placing live copepods in a narrow parallel-sided glass cell with outside dimensions of 50 × 50 × 10 mm and walls 1.5 mm thick. The cell was filled with filtered sea water and placed on a raised platform at a convenient height for photography using a camera aimed at it horizontally. To help with the alignment, the camera was placed on a laboratory jack in front of the tank. The tank was illuminated from one side by a fiber optic light fitted with a color filter suited to bring its color temperature to that of daylight (~5,500°K). An Olympus OM 2n camera set in automatic mode was used with B/W Ilford XPI film. It was fitted with a Panagor 90 mm 2.8 AutoMacro Lens, and to give increased magnification, a ×2 teleconverter was added. The camera was connected to an Olympus T20 flash gun placed directly above and close to the top of the cell and was used on TTL centralized control mode (automatic exposure). An automatic winder (winder 2 with a mains power unit) was attached to the camera to help with quick sequence shots. The whole apparatus was used in a constant temperature room (8°C) with no room lighting. This apparatus permitted photographs of live animals with appendages and body posture in the natural orientation.

Setal lengths were measured at the Smithsonian Oceanographic Sorting Center on formaldehyde-fixed adult females of *Euchaeta antarctica*, *E. norvegica*, and *E. rimana*. Measurements were made with a camera lucida attachment on a Wild M5A dissecting microscope.

## RESULTS

Detailed examination of the structure and natural posture of the first antennae of the live adult female *Euchaeta norvegica* shows that this copepod has a distinctive setal array on the first antenna. Along the entire length of the antenna there are straight setae of varying lengths that point anteriorly during swimming (Fig. 1). At the distal tip of the antenna of adult female *E. norvegica* there are 2 elongate setae and a feathered seta oriented toward the posterior end of the copepod.

On the seventh and eighth free antennal segments, there is one curved elongate seta per segment, each oriented at right angles to the plane of the main antennae (Fig. 2) and perpendicular to the plane of the pre-

viously described straight setae (Fig. 3). The seta on segment 7 curves ventrally, while the seta on the eighth segment curves dorsally. To either side of this pair of setae, on segments 3 and 13, there are 2 elongate straight setae oriented anteriorly. These and the 2 curved setae form a 4-point quadrangular array oriented into the fluid ahead of the copepod. This array, as well as other setae, line both antennae (Fig. 4).

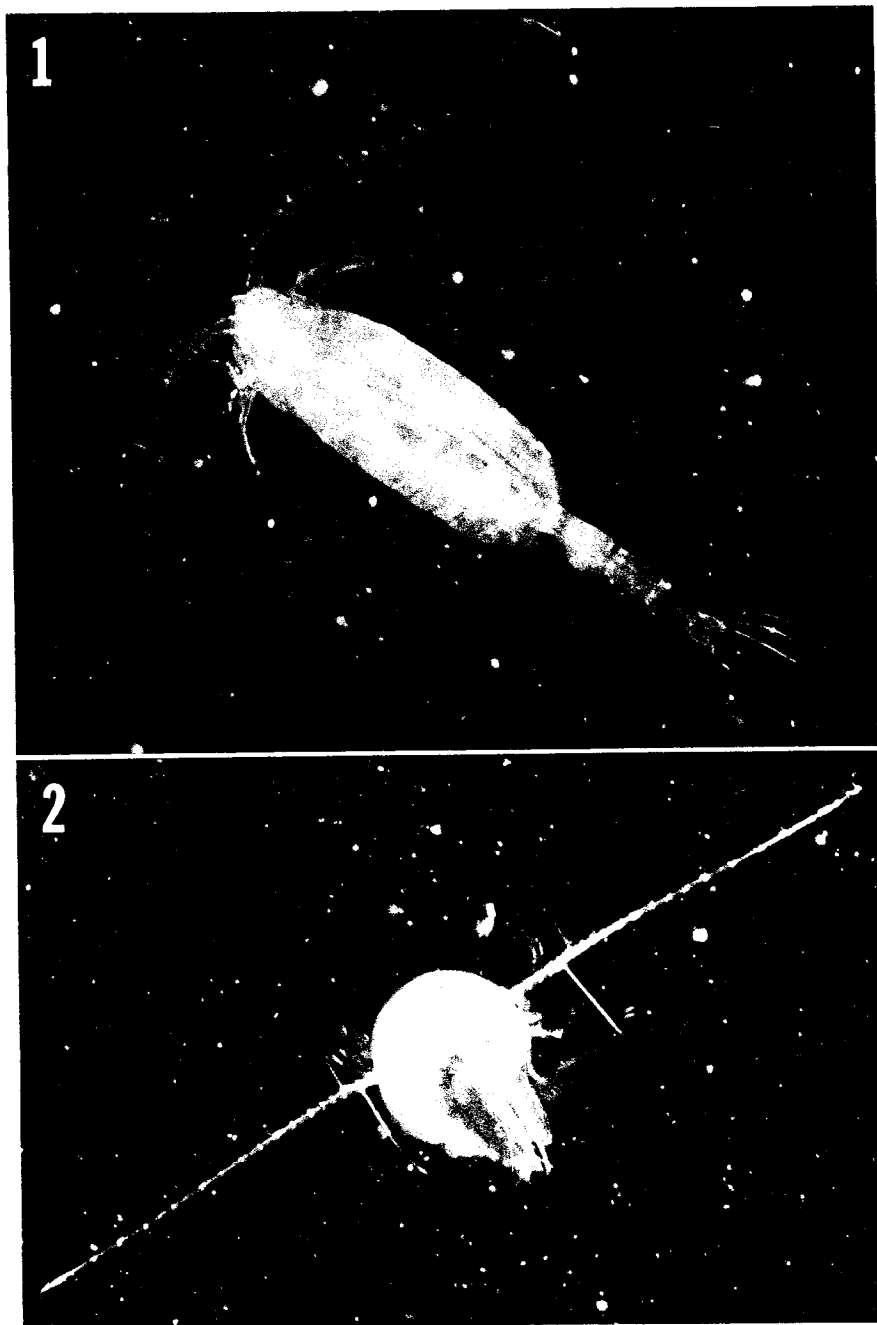
Lengths of the setae in this 4-point array were measured for three species of *Euchaeta* (Table 1). The 2 curved setae on segments 7 and 8 were longer than the 2 straight ones on segments 3 and 13. The resultant 4-point quadrangular array, however, projects with the setal tips equidistant from the face of the first antennae (see profile in Fig. 4).

Little change in the conformation of the 4-point array was seen in the live copepods. However, setae on preserved animals often are bent distally and lie flat against the antenna; this conformation was never seen in the live copepods.

## DISCUSSION

### Paired Setal Array on First Antennae

Models of chemosensory (Andrews, 1983) and mechanosensory (Legier-Visser *et al.*, 1986) detection by copepods along with studies of threshold sensitivities of zooplankton to various stimuli (Gill, 1985; Kirk, 1985; Newbury, 1972; Poulet and Ouellet, 1982) and detailed morphological descriptions of the chemo- and mechanosensory receptors (Fleminger, 1985; Friedman, 1980; Friedman and Strickler, 1975; Gill, 1986; Markl, 1978; Mauchline, 1977; Strickler and Bal, 1973; Strickler, 1975a, b) have allowed a better understanding of a sensor's functional morphology and the stimulus levels in the environment that are needed to elicit responses by zooplankton. Recently, attention has shifted from chemosensory responses (Hamner and Hamner, 1977; Poulet and Ouellet, 1982) to analyzing mechanosensory reception (Gill, 1985; Gill and Crisp, 1985; Hauray *et al.*, 1980). Buskey (1984) commented that the physical presence of phytoplankton in the water column may be as important to early detection as the chemical signals excreted by the phytoplankton. Early detection of particles increases the probability of particle capture



Figs. 1, 2. Live *Euchaeta norvegica* freely swimming in a small tank. Fig. 1. Dorsal view. Note paired antennae extending to either side of the copepod with proximal setae extending in the forward direction and distal setae extending posteriorly. Fig. 2. Head-on view. Note setae close to either side of the copepod's body that are oriented at right angles to the plane of antennae and the plane of setae described in Fig. 1.

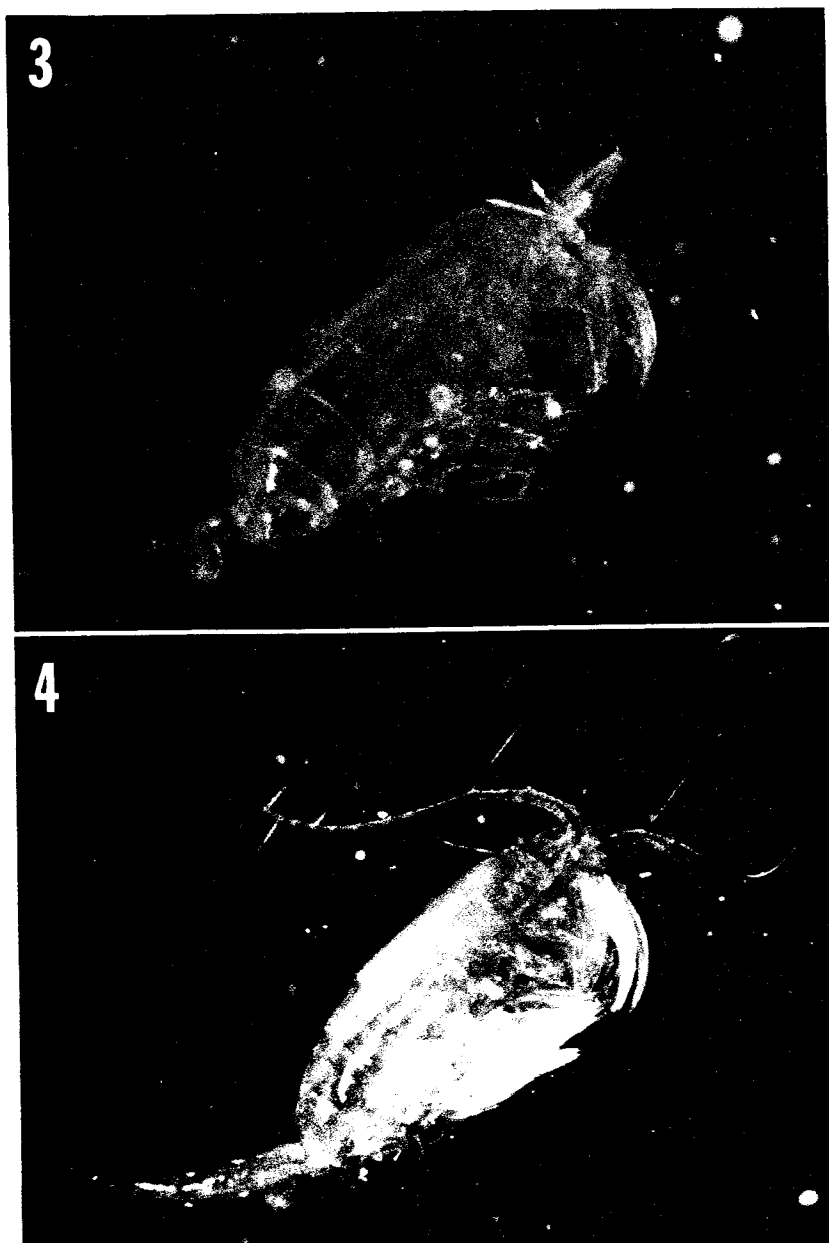
by effectively increasing the time during which the copepod reorients for optimal particle capture (Andrews, 1983). Information on reactive distances and perceptive fields of copepods (Kerfoot *et al.*, 1980; Newbury, 1972) helps to specify cues to

which the copepods are reacting in order to remotely detect the presence of their food versus predators or mates in the water.

Yet in order to understand the function of the sensors, detailed examination must be made of their morphology. Here, we have

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Figs. 3, 4. Live *Euchaeta norvegica* freely swimming in a small tank. Fig. 3. Side view. Note elongate curved setae oriented in the forward direction. Fig. 4. Conformation of setae on the first antennae showing paired 4-point array of elongate straight and curved setae along the antennae on either side of the copepod's body. Setal tips of the array extend equidistant from the face of the antenna.

described an elegant setal array on the first antennae of *Euchaeta*. The unique orientation and lengths of straight and curved setae as well as the distance between setae along the antennae may be specifically sensitive to certain frequencies of motion. A copepod may be able to distinguish shape as well as dimensions of an oncoming par-

ticule and, thus, tailor its behavioral response to the particle in terms of this early sensory information (Legier-Visser *et al.*, 1986). In fact, descriptions of the fluid flow around the subtropical *E. rimana* (Yen, personal observation) show that the setae are aligned parallel to the flow field and thus are well positioned for detecting deformations in the

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Table 1. Lengths ( $\mu\text{m} \pm \% \text{ standard error}$ ,  $N = \text{number of observations}$ ) of the prosome (PL), first antenna (A1), and setae on the articulated antennular segments 3 (s3), 7 (s7), 8 (s8), and 13 (s13) of 3 species of *Euchaeta*.

	<i>E. norvegica</i> from 36°55'N, 74°15'W	<i>E. rimana</i> from 6°55'S, 150°8'W	<i>E. antarctica</i> from 56°50'S, 34°20'W
PL	5,557 $\pm$ 4.9%, $N = 11$	2,316 $\pm$ 3.6%, $N = 8$	6,837 $\pm$ 4.5%, $N = 8$
A1	5,994 $\pm$ 4.0%, $N = 20$	2,669 $\pm$ 3.2%, $N = 26$	7,311 $\pm$ 3.4%, $N = 20$
s3	1,282 $\pm$ 6.3%, $N = 20$	699 $\pm$ 5.2%, $N = 20$	1,403 $\pm$ 8.9%, $N = 9$
s7	2,480 $\pm$ 3.7%, $N = 17$	1,324 $\pm$ 4.1%, $N = 12$	2,881 $\pm$ 6.5%, $N = 11$
s8	2,356 $\pm$ 2.3%, $N = 8$	1,128 $\pm$ 9.6%, $N = 10$	2,470 $\pm$ 5.1%, $N = 5$
s13	1,624 $\pm$ 3.6%, $N = 13$	915 $\pm$ 5.7%, $N = 13$	1,767 $\pm$ 5.8%, $N = 12$

streamlines. With this paired specialized structure, hydrodynamic disturbances may be detected and spatially located along all 3 planes, with each sensor possibly responding to a single component of velocity. Moreover, the use of spatially arranged receptors has been suggested as important in locating objects in space (e.g., Suckling, 1967). The multidirected array of mechanoreceptive setae characteristic of the first antennae of copepods may thus be used to receive and analyze signals from several directions independently (Friedman, 1980).

This setal array is found on at least 4 species of *Euchaeta* (*rimana*, *elongata*, *norvegica*, and *antarctica*; Yen, personal observation). The array is more structurally elaborate than that found on herbivorous copepods in the family Calanidae (Fleminger, 1985). Adult males of *Euchaeta* lack the elongate setae, which they lose when they molt into their final adult stage. Their antenna 2, mandible, maxilla 1, maxilla 2, and maxilliped are reduced in size of segments and setae; the gnathobase of the mandible and inner lobe 1 of maxilla 1 are reduced in size, and the mandibular teeth and lobe 1 spines are undeveloped (Ferrari, personal communication). The males do not feed with these degenerate mouthparts and therefore may not need such elaborate antennular setation. Without their first antennae, adult females of *E. norvegica* survived for at least a month, yet did not feed (Yen, 1987); the antennae apparently were needed to detect prey as has been shown for other copepods (Gill, 1986; Landry, 1980; Mullin, 1967; Yen, 1982a).

#### Remote sensing by *Euchaeta*

The greater importance of mechanical cues over visual and chemical cues has been evaluated for adult female stages of *Euchaeta*. Visual cues require light for detec-

tion. *Euchaeta elongata*, the temperate species, feeds in the dark (Yen, 1982a). It does not depend on visual cues for prey detection. In a very simple experiment to test the response to chemical cues, Yen (1982a) found that the addition of a chemical exudate (a homogeneous mixture of filtered sea water with the 60- $\mu\text{m}$  mesh filtrate of crushed prey, adults of *Aetideus divergens*) did not reduce or enhance feeding rates of *E. elongata* on that same prey, suggesting that chemosensory perception may not be as important as other types of stimuli.

Instead, members of the genus *Euchaeta* appear to find their mobile prey by mechanosensitive perception of hydrodynamic signals generated by the prey's swimming and feeding movements. We base this conclusion on the following results: through measurements of changes in feeding rates in response to various stimuli, *Euchaeta* exhibits size-selective nighttime predation only on active prey (Yen, 1982, 1985); they do not consume heat-killed copepods, which do not move, nor small prey, such as copepod nauplii which are hydrodynamically inconspicuous because of their small size and reduced movement. Small prey also may be inefficiently handled, although personal observations (Yen) indicate that *Euchaeta* may not even handle nauplii, since the nauplii can nearly touch the setae of *Euchaeta* without eliciting an attack response.

Within the size range of preferred copepod prey ( $\sim 1$  mm in prosome length), feeding rates of *E. elongata*, the temperate species, were low on *Acartia* or *Oithona* and higher on *Pseudocalanus* (Yen, 1985). *Acartia* and *Oithona* are intermittent swimmers, with short-duration darting movements at high swimming speeds followed by periods of quiescence when they do not move and are not detectable by *Euchaeta* (Yen, 1988). *Pseudocalanus*, on the other hand, swims

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constantly, and continuously generates hydrodynamic disturbances which may account, in part, for higher predation rates on this type of prey. Predation rates also were low on weakly swimming early yolk sac fish larvae which create little water disturbance and were high on more active swimmers which still have a poorly developed escape response (Bailey and Yen, 1983), giving further support to the suggestion that *Euchaeta* hunts by mechanoreceptive prey detection.

According to Strickler (1982), *Euchaeta russelli* swims exclusively in a cruising mode that generates no anterior double shear field in front of its mouthparts, which, thus, is advantageous for mechanoreception. Gerritsen (1980) found that males of *Cyclops* pursue females in a response that is too quick to be chemically induced and therefore must be a reaction to mechanical disturbances caused by the swimming female. Zaret and Kerfoot (1980) also observed that the small fresh-water cladocerans *Bosmina*, are less readily detected when akinetic.

The determination of the means by which copepods detect their prey, be it visual, chemical, or mechanical perception, and the characteristic signals produced by their prey versus predators or mates, will advance our understanding of copepod communication and the remote sensing of underwater disturbances. As has been recently determined for other marine copepods (Yen *et al.*, personal observation), the antennular setae, indeed, are extremely sensitive to mechanical disturbances. Such a setal array on the first antennae of the carnivorously feeding stages of *Euchaeta* may be specialized for remote detection of the movements in water of active copepod prey.

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#### LITERATURE CITED

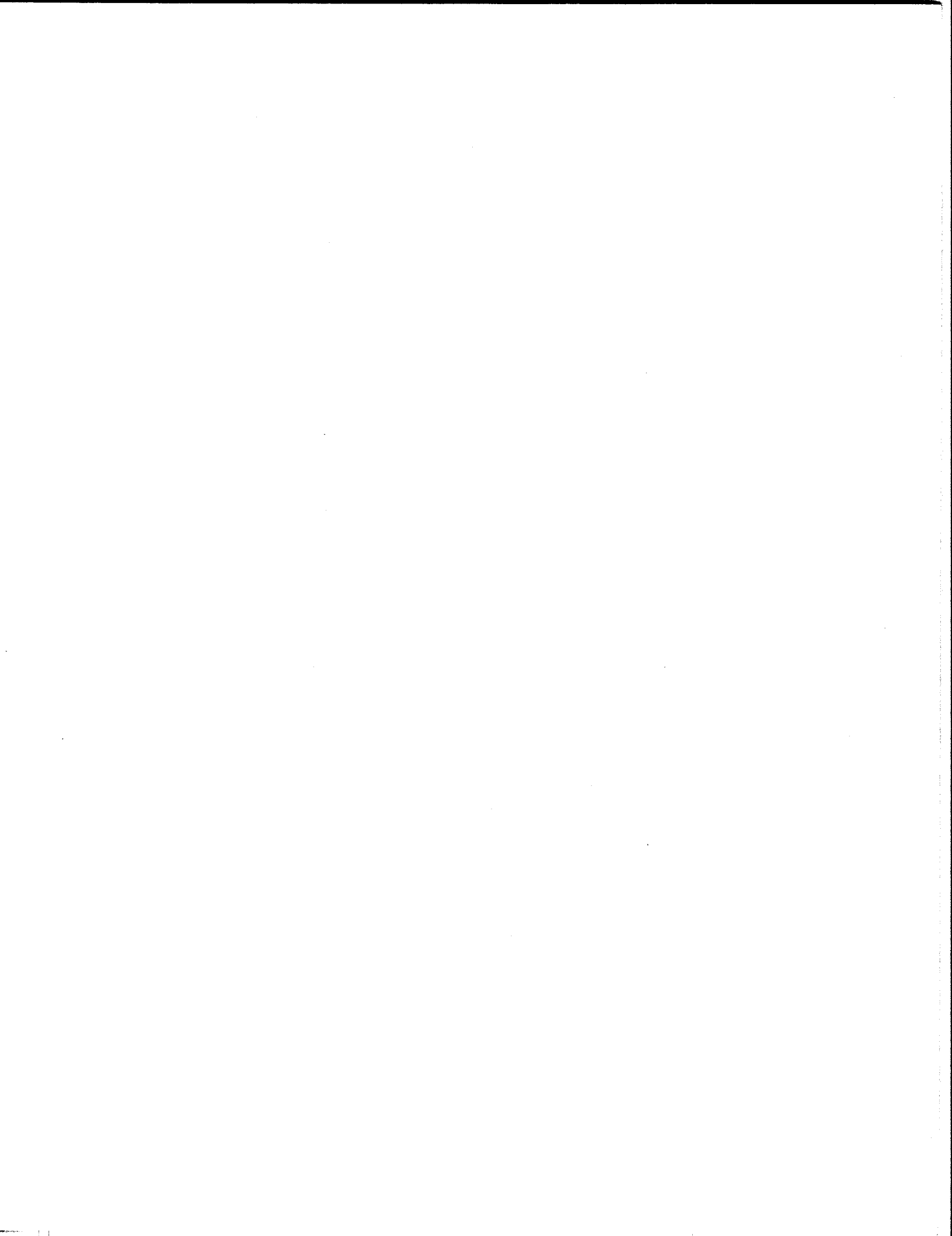
- Andrews, J. C. 1983. Deformation of the active space in the low Reynolds number feeding current of calanoid copepods. — *Canadian Journal of Fisheries and Aquatic Sciences* 40: 1293–1302.
- Bailey, K. M., and J. Yen. 1983. Predation by a carnivorous marine copepod, *Euchaeta elongata* Esterly, on eggs and larvae of the Pacific hake, *Merluccius productus*. — *Journal of Plankton Research* 5: 71–82.
- Båmstedt, U., and M. R. Holt. 1978. Experimental studies on the deepwater pelagic community of Korsfjorden, western Norway: prey-size preference and feeding of *Euchaeta norvegica* (Copepoda). — *Sarsia* 63: 225–236.
- , and H. J. Skjoldal. 1976. Studies on the deepwater pelagic community of Korsfjorden, western Norway. Adenosine phosphate and nucleic acids in *Euchaeta norvegica* (Copepoda) in relation to its life cycle. — *Sarsia* 60: 63–80.
- Buskey, E. J. 1984. Swimming pattern as an indicator of the roles of copepod sensory systems in the recognition of food. — *Marine Biology* 78: 53–57.
- Fleminger, A. 1985. Dimorphism and possible sex change in copepods of the family Calanidae. — *Marine Biology* 88: 273–294.
- Friedman, M. M. 1980. Comparative morphology and functional significance of copepod receptors and oral structures. — *In*: W. C. Kerfoot, ed., *Evolution and ecology of zooplankton communities*. Pp. 185–197. University Press of New England, Hanover, New Hampshire.
- , and J. R. Strickler. 1975. Chemoreceptors and feeding in calanoid copepods (Arthropoda: Crustacea). — *Proceedings of the National Academy of Sciences* 72: 4185–4188.
- Gerritsen, J. 1980. Adaptive responses to encounter problems. — *In*: W. C. Kerfoot, ed., *Evolution and ecology of zooplankton communities*. Pp. 52–62. University Press of New England, Hanover, New Hampshire.
- Gill, C. W. 1985. The response of a restrained copepod to tactile stimulation. — *Marine Ecology-Progress Series* 21: 121–125.
- . 1986. Suspected mechano- and chemosensory structures of *Temora longicornis* (Copepoda: Calanoida). — *Marine Biology* 93: 449–457.
- , and D. J. Crisp. 1985. Sensitivity of intact and antennule amputated copepods to water disturbance. — *Marine Ecology-Progress Series* 21: 221–227.
- Hamner, P., and W. M. Hamner. 1977. Chemosensory tracking of scent trails by the planktonic shrimp *Acetes sibogae australis*. — *Science* 195: 886–888.
- Haury, L. R., D. E. Kenyon, and J. R. Brooks. 1980. Experimental evaluation of the avoidance reaction of *Calanus finmarchicus*. — *Journal of Plankton Research* 2: 187–202.
- Hopkins, T. L. 1985. The zooplankton community of Croker Passage, Antarctic Peninsula. — *Polar Biology* 4: 161–170.
- Kerfoot, W. C., D. C. Kellogg, Jr., and J. R. Strickler. 1980. Visual observations of live zooplankters: evasion, escape and chemical defenses. — *In*: W. C. Kerfoot, ed., *Evolution and ecology of zooplankton communities*. Pp. 10–27. University Press of New England, Hanover, New Hampshire.
- Kirk, K. L. 1985. Water flows produced by *Daphnia* and *Diaptomus*: implications for prey selection by mechanosensory predators. — *Limnology and Oceanography* 30: 679–686.
- Landry, M. R. 1980. Detection of prey by *Calanus pacificus*: implications of the first antennae. — *Limnology and Oceanography* 25: 545–549.
- Legier-Visser, M. F., J. G. Mitchell, A. Okubo, and J.

- A. Fuhrman. 1986. Mechanoreception in calanoid copepods.—*Marine Biology* 90: 529–535.
- Lowndes, A. G. 1935. The swimming and feeding of certain calanoid copepods.—*Proceedings of the Zoological Society of London* 1935: 687–715.
- Markl, H. 1978. Adaptive radiation of mechanoreception.—*In: M. A. Ali, ed., Sensory ecology: review and perspectives*. Pp. 319–344. Plenum Press, New York, New York.
- Mauchline, J. 1977. The integumental sensilla and glands of pelagic Crustacea.—*Journal of the Marine Biological Association of the United Kingdom* 57: 973–994.
- McGowan, J. A., and P. W. Walker. 1979. Structure in the copepod community of the North Pacific central gyre.—*Ecological Monographs* 49: 195–226.
- Mullin, M. M. 1967. On the feeding behavior of planktonic marine copepods and the separation of their ecological niches.—*Proceedings of the Symposium on Crustacea; Ernakulam, Marine Biological Association of India* 3: 955–964.
- Newbury, T. K. 1972. Vibration perception by chaetognaths.—*Nature* 236: 459–460.
- Ohman, M. D., B. W. Frost, and E. B. Cohen. 1983. Reverse diel migration. An escape from invertebrate predators.—*Science* 220: 1404–1407.
- Poulet, S. A., and G. Ouellet. 1982. The role of amino acids in the chemosensory swarming and feeding of marine copepods.—*Journal of Plankton Research* 4: 341–361.
- Strickler, J. R. 1975a. Intra- and interspecific information flow among planktonic copepods: receptors.—*Verhandlungen der internationalen Vereinigung für theoretische und angewandte Limnologie* 19: 2951–2958.
- . 1975b. Swimming of planktonic Cyclops (Copepoda, Crustacea): pattern, movements and their control.—*In: T. Y.-T. Wu, ed., Swimming and flying in nature*. Vol. 2, pp. 599–616. Plenum Press, New York, New York.
- . 1982. Calanoid copepods, feeding currents, and the role of gravity.—*Science* 218: 158–160.
- , and A. K. Bal. 1973. Setae of the first antennae of the copepod *Cyclops scutifer* (Sars): their structure and importance.—*Proceedings of the National Academy of Sciences* 70: 2656–2659.
- Suckling, E. E. 1967. Electrophysiological studies on the trunk lateral line system of various marine and fresh water teleosts.—*In: P. H. Cahn, ed., Lateral line detectors*. Pp. 97–103. Indiana University Press, Bloomington, Indiana.
- Yen, J. 1982a. Sources of variability in attack rates of *Euchaeta elongata* Esterly, a carnivorous marine copepod.—*Journal of Experimental Marine Biology and Ecology* 63: 105–117.
- . 1982b. Predatory feeding ecology of *Euchaeta elongata* Esterly, a carnivorous marine copepod.—Ph.D. thesis, University of Washington, Seattle, Washington. Pp. 1–141.
- . 1983. Effects of prey concentration, prey size, predator life stage, predatory starvation and season on predation rates of the carnivorous marine copepod *Euchaeta elongata*.—*Marine Biology* 75: 69–77.
- . 1985. Selective predation by the carnivorous marine copepod *Euchaeta elongata*: laboratory measurements of predation rates verified by the field observations of temporal/spatial feeding patterns.—*Limnology and Oceanography* 30: 577–597.
- . 1987. Predation by *Euchaeta norvegica* Boeck on eggs and larvae of the Norwegian cod *Gadus morhua* L.—*Journal of Experimental Marine Biology and Ecology* 112: 283–296.
- . 1988. Directionality and swimming speeds in predator-prey and male-female interactions of *Euchaeta rimana*, a subtropical marine copepod.—*Bulletin of Marine Science* 43: 175–193.
- Zaret, R. E., and W. C. Kerfoot. 1980. The shape and swimming technique of *Bosmina longirostris*.—*Limnology and Oceanography* 25: 126–133.

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

Jeannette Yen

## 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  $7 \text{ mm} \cdot \text{s}^{-1}$ , 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). Similarly, 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 swimming 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 carnivorous (Båmstedt and Holt, 1978; Yen, 1985). In the subtropical waters surrounding 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 abundance 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- $\mu$ m 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 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- $\mu$ m prosome length) for food. These small copepods were collected using a 110- $\mu$ m-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 following 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 Schlieren optical pathway as designed by Toepfer (1866) in which an object forms a light image on a dark background. The light energy of 0.1  $\mu$ W  $\cdot$  cm<sup>-2</sup> 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<sup>-1</sup>. The activity of the copepods was recorded in the dark, in a tank of the following dimensions: 12 x 12 x 15 cm (length x width x 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- $\mu$ m 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  $\pm 10^\circ$ .

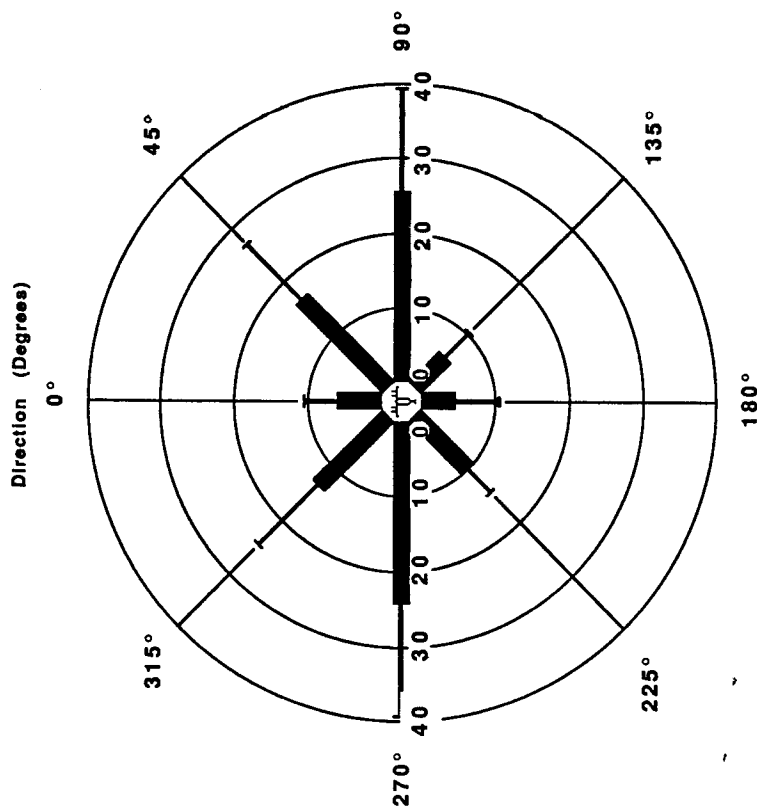


Figure 1. Directional swimming exhibited by adult *Euchaeta rimana* demonstrating a strong horizontal component. Six different females collected from 3 different dates were analyzed for at least 50 sec each for a total swimming time of 713 sec. The mean percent time spent swimming ( $\pm 95\%$  C.I.;  $N = 6$ ) 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  $7.06 \pm 0.35$  mm  $\cdot$  sec<sup>-1</sup> (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

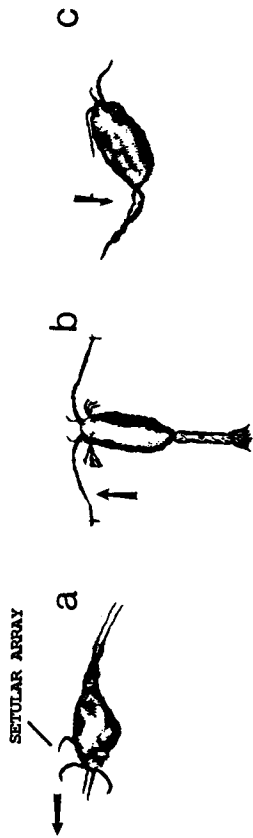


Figure 2. Digitized images from videotapes of *Euchaeta rimana*. Arrow denotes direction of motion. (a) Adult female swimming. Note the orientation of setular array on first antennae into water not disturbed by self-generated hydrodynamic motion. (b) Adult male swimming. Note orientation of slim body 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 used its 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  $2.6 \pm 0.34$  s (95% C.I.,  $N = 180$ ) in the 12 cm x 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  $142 \text{ mm} \cdot \text{s}^{-1}$  or 60 body lengths  $\cdot \text{s}^{-1}$  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  $\cdot \text{s}^{-1}$  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 ( $0^\circ$ ,  $180^\circ$ ) component (Fig. 3). The males swam up with their long axis of the body aligned with the flow (Fig. 2b) at a speed of  $7.5 \pm 0.4 \text{ mm} \cdot \text{s}^{-1}$  (95% C.I.,  $N = 11$ ) and sank with their ventral surface down and urosome arched (Fig. 2c) at a speed of  $5.0 \pm 0.4 \text{ mm} \cdot \text{s}^{-1}$  (95% C.I.,  $N = 11$ ). Escape speeds can reach up to  $360 \text{ mm} \cdot \text{s}^{-1}$  or 150 body lengths  $\cdot \text{s}^{-1}$  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

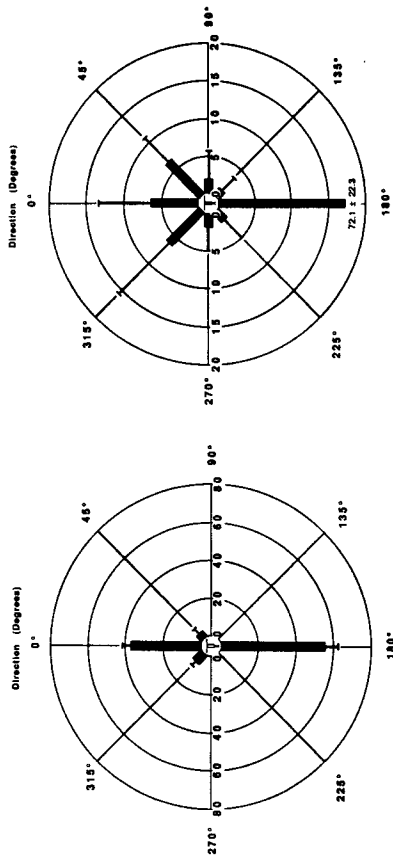


Figure 3. Directional swimming exhibited by adult male *Euchaeta rimana* demonstrating a strong vertical component. Seven different males collected from three different dates were analyzed for 20 to 130 sec each for a total swimming time of 465 sec. The mean percent time spent swimming ( $\pm 95\%$  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 ( $\pm 95\%$  C.I.,  $N = 4$ ) in each direction is shown. Value on  $180^\circ$  bar represents mean per cent time  $\pm 95\%$  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  $87 \text{ mm} \cdot \text{s}^{-1}$ , 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 ( $0.35$ - $1 \text{ mm}$  prosome length) swam with a rhythmic motion, resting for  $83 \pm 31$  ms ( $N = 22$ ) followed by short jumps at speeds averaging  $10 \text{ mm} \cdot \text{s}^{-1}$  or  $27.2 \pm 5.0$  body lengths  $\cdot \text{s}^{-1}$  ( $N = 23$ ; 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  $43.5 \text{ mm} \cdot \text{s}^{-1}$  or  $17.4$  body lengths  $\cdot \text{s}^{-1}$  for a 2.5 mm predator. The lunge motivated an escape by the prey at  $64.5 \text{ mm} \cdot \text{s}^{-1}$  or 107 body lengths  $\cdot \text{s}^{-1}$  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  $129 \text{ mm} \cdot \text{s}^{-1}$  or 215 body lengths  $\cdot \text{s}^{-1}$ . 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 Nicol, submitted). Prior to capture, the predatory copepod must first en-

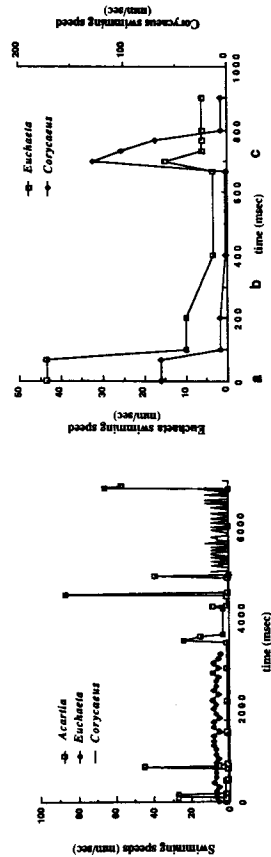


Figure 5. Variation in swimming speeds exhibited by three copepods: *Euchaeta rimana* (2.5 mm Prosome Length)—smooth continuous swimming at an average speed of 7 mm·sec<sup>-1</sup>, *Acartia* (0.7 mm PL)—high speed darting (up to 90 mm·sec<sup>-1</sup>) with 1–2 sec intervals of sinking, *Corycaeus* (0.35 mm PL)—high speed darting at 10 mm·sec<sup>-1</sup> 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<sup>-1</sup> made *Corycaeus*, which is 2.1 mm away (distance between tips of their prosomes), dart away at 64.5 mm·sec<sup>-1</sup>, increasing the distance between the predator and prey to 3.5 mm. b) *Corycaeus* drifted slowly away at a speed of 1 mm·sec<sup>-1</sup> while *E. rimana* continued to swim in its direction at a cautious speed of 3.5 mm·sec<sup>-1</sup>. When *E. rimana* was 3.7 mm away from the cyclopid 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<sup>-1</sup>. This time, *Corycaeus* darted away at a speed of 129 mm·sec<sup>-1</sup> 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 to 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 zooplankton 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.

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.

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<sup>1</sup> J. Yen and N. T. Nicoll. The structure of the first antennae of a carnivorous marine copepod *Euchaeta norvegica*, early detection of active prey using a mechanoreceptive detector. Mar. Biol. Submitted.

## 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.
- Busley, 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* Kroyer 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.
- Haurly, 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. Ueber die Methode der Schlierenbeobachtung als mikroskopisches Hilfsmittel, nebst Bemerkungen zur Theorie der schiefen Beleuchtung. *Poggendorff'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.

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## 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.