

## Implications of the feeding current structure of *Euchaeta rimana*, a carnivorous pelagic copepod, on the spatial orientation of their prey

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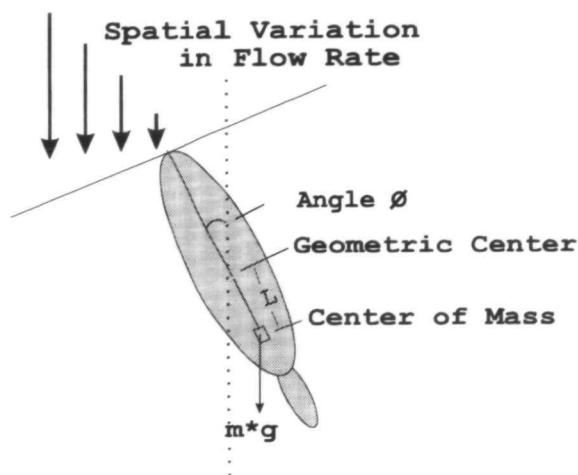
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**Abstract.** Many marine planktonic organisms create water currents to entrain and capture food items. Rheotactic prey entrained within these feeding currents often exhibit escape reactions. If the direction of escape is away from the feeding current, the prey may successfully deter predation. If the escape is towards the center of the feeding current, the prey will be re-entrained towards its predator and remain at risk of predation. The direction of escape is dependent on (i) the ability of the prey to escape in a direction different than its pre-escape orientation and (ii) the orientation caused by the interaction of the prey's body with the moving fluid. In this study, the change in orientation of *Acartia hudsonica* nauplii as a result of entrainment within the feeding current of *Euchaeta rimana*, a planktonic predatory copepod, was examined. When escaping in still water, *A. hudsonica* nauplii were able to vary their pre-escape direction by only 10°. This allows only a limited ability to escape in a direction different than their pre-escape orientation. Analyses of the feeding current of *E. rimana* show the flow speed to be most rapid in the central region with an exponential decrease in speed distally. In contrast, flow vorticity is minimal in the center of the feeding current and maximal at 1.75 mm along the antennae. As a result, the degree of rotation of the prey towards the center of the feeding current shows a strong dependency on the prey's location within the feeding current. The feeding current of *E. rimana* rotated the prey 14° when near the center of the flow field and up to 160° when located more distal in the feeding current. Since the prey's escape abilities cannot compensate for the rotation due to the flow, this mechanism will maintain the escaping prey within the feeding current of their predator. Therefore, the feeding current facilitates predatory copepods in capturing prey by (i) increasing the amount of water which passes over their sensors and through their feeding appendages and (ii) controlling the spatial orientation of their prey prior to escape.

### Introduction

An important component often ignored in predator–prey interactions among copepods is the spatial orientation of the prey in relation to its predator. Yet the prey's orientation can have a profound effect on its ability to detect fluid disturbances (Haury *et al.*, 1980) and control the direction of the escape once it is initiated. The prey's escape direction will determine whether it leaps out of the predator's capture region, is retained within the capture region or is directed from the periphery towards the capture area. Therefore, characterizing the spatial orientation of organisms is critical to interpreting predator–prey interactions among copepods and, in particular, in predicting the success of prey escaping predation.

The orientation adopted by marine copepods in relation to their surroundings is not random. The orientation is due to either behavioral characteristics and/or the result of the interaction between the morphology of the organism and a particular fluid dynamic environment (Kessler, 1985). For example, the stable sinking orientation of a marine copepod arises from the balance of two forces (Figure 1). These forces are a rotational force which results from the separation of the center of mass and the geometric center of the animal (in other words,



**Fig. 1.** Balance of two rotational forces acting on a copepod entrained within a sheared flow. In still water, the animal's orientation is determined by the separation ( $L$ ) of the geometric center (GC) and the center of mass (CM). Within a sheared flow field, the animal is rotated towards the region of highest flow as a result of water traveling at different speeds striking different parts of the body. The final orientation will be a balance between the rotational force due to the separation of the GC from the CM with that derived from the sheared flow.

the animal is bottom heavy), and the frictional force which results from the interaction between the organism and its surrounding viscous fluid (Vogel, 1981; Jonsson *et al.*, 1991). In an environment in which the fluid is moving relative to the organism, their orientation can be dependent on the local hydrodynamics. Many aquatic organisms cause fluid motion either to entrain food, sample their surroundings, or to move through the water. Kessler (1985) demonstrated that a spherical cell will obtain a stable swimming direction different from the vertical if the rotation due to the local hydrodynamics balances that caused by the asymmetrical distribution of mass within the organism. Prey entrained within the feeding current of predatory copepods are subject to the same source of torque, potentially causing them to be rotated from their stable orientation. To calculate the orientation requires two pieces of information: (i) a fine-scale analysis of the fluid environment surrounding the entrained prey; (ii) determination of the distribution of mass within the entrained prey. To relate the prey's final orientation to the escape direction requires knowledge on the ability of the prey to escape in a direction different from its pre-escape orientation.

Three possible scenarios concerning the prey's orientation can be envisioned: (i) the orientation remains stationary as a result of the overpowering effect of the displacement of mass in the prey; (ii) the orientation reflects a balance between the prey's morphology and the predator's feeding current (i.e. Kessler's system); (iii) the entrained prey tumbles at a rate controlled primarily by the flow characteristics. In the latter case, the orientation is determined by the rate of rotation and the duration of advection which continues until the escape reaction is elicited.

In this study, I investigate a previously undescribed mechanism by which the orientation and escape direction of potential prey are varied by the feeding current of their predators. The orientation of *Acartia hudsonica* nauplii is examined when entrained within a feeding current of the predatory copepod *Euchaeta rimana*. When feeding, *E. rimana*, a predatory marine copepod (Finn, 1983; Doall, 1995), entrains prey by creating a laminar flow feeding current (Yen *et al.*, 1991), as do the omnivorous copepods *Pleuromamma* sp. (Fields and Yen, 1993), *Temora* sp. (Yen and Fields, 1992), and other marine and freshwater copepods (Strickler, 1985; Paffenhofer and Lewis, 1990). Adult females of this species exhibit two types of foraging strategies: hovering and cruising. Doall and Yen (1995) suggest that only during hovering does the predator use the feeding current to entrain potential prey. Herein, the role of *E. rimana*'s feeding current generated in a hovering position in controlling the spatial orientation of potential prey is determined. Both theoretical and laboratory data are presented and discussed in relation to implications for predator avoidance and prey capture among copepods.

## Method

### *Study organisms*

The flow-generating organism used in this study was the calanoid copepod *E. rimana* (2.5 mm). The animals were captured on 18 January 1992 by gently towing a 330 mm net for 5–10 min in the surface waters ~1.5 km offshore of Oahu, Hawaii, in Kanehoe Bay. In the laboratory, the animals were sorted and packaged for transport to the State University of New York (SUNY) at Stony Brook. Healthy female specimens were then separated and tethered (Yen and Fields, 1992) and allowed to acclimate to the filming vessel (125 ml: 5 cm<sup>3</sup>) for at least 3 h.

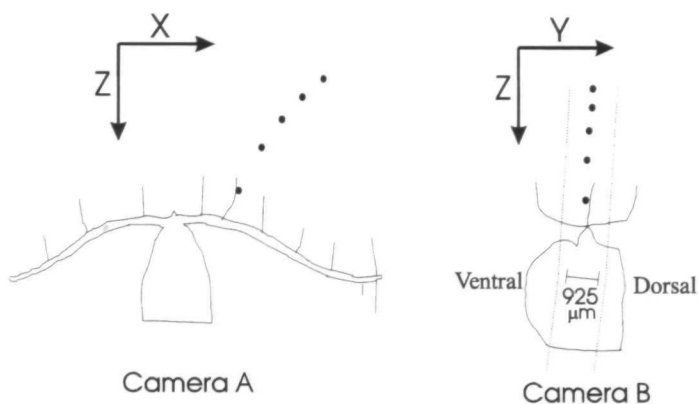
*Acartia hudsonica* were collected on 19 January 1992 from Stony Brook Harbor, NY, using a 64 mm net towed at the surface for 5–7 min and then quickly transported to the laboratory. *Acartia* nauplii were sorted and then allowed to acclimate to 18°C for 24–36 h prior to filming.

### *Filming apparatus*

Filming was carried out at SUNY Stony Brook on an apparatus which replicates the optical path described by Strickler (1985). The set-up is a modified schlieren optical light path with a split light source that cross perpendicular to each other before passing to two perpendicularly mounted Pulnix video cameras (Yen and Fields, 1992).

### *Analysis of Euchaeta feeding current*

Velocity and vorticity contours of the feeding current of *E. rimana* were mapped for the region above the first antennae (the location of the majority of prey escapes) using 20 µm polystyrene spheres (Polyscience) as tracers of the fluid



**Fig. 2.** Planar views from two perpendicularly mounted cameras. Only particles and prey which maintained their trajectory within the corridor shown in camera B were followed in camera A. By minimizing the volume of water analyzed, the feeding current could be treated as a two-dimensional flow.

motion. Individual particle locations were recorded at various time intervals using a Cartesian coordinate system. The  $XZ$  coordinates were taken from one camera, while the  $YZ$  coordinates were taken from the other camera (Strickler, 1985; Yen and Fields, 1992; Fields and Yen, 1993) (Figure 2). Using only those particles which shared a common  $Y$  value ( $\pm 925 \mu\text{m}$ ; maintaining a trajectory for at least one body length in the  $Z$  direction along the sagittal plane), an essentially planar view of the feeding current was mapped. Water velocity ( $V$ ) at each point above the first antennae was calculated by:

$$V = (U^2 + W^2)^{1/2}$$

with  $U$  describing the velocity in the  $X$  direction and  $W$  describing the velocity in the  $Z$  direction. Since only those particles which maintained their trajectories within a narrow corridor were used, the added velocity due to motion in the  $Y$  direction could be ignored. The maximum error associated with such a calculation is the increase in the distance traveled if the particle trajectory was from the upper corner of the corridor down to the opposite corner at the bottom of the corridor as compared to traveling straight down the corridor. Since such a narrow corridor was used, the maximum error in the present study is  $<4\%$ .

Isolines of equal water flow magnitude were computed using the contouring program SURFER 4.01.

Vorticity ( $V_o$ ) of the feeding current in two dimensions was calculated as:

$$V_o = \left( \frac{\delta U}{\delta z} \right) - \left( \frac{\delta W}{\delta x} \right)$$

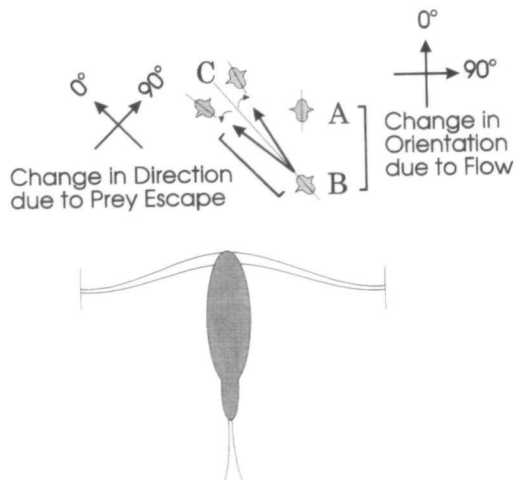
with  $U$  describing the velocity in the  $X$  direction and  $W$  describing the velocity in the  $Z$  direction. The grid spacing used to calculate the variations in velocity was  $\sim 250 \mu\text{m}$  which is roughly equivalent to 1.5 times the size of the average prey.

### Orientation of *Acartia* in still water

The orientation of *A. hudsonica* nauplii in still water was recorded using the filming apparatus described above. *Acartia hudsonica* have been reported to have a 'hop and sink' swimming behavior (Tiselius and Jonsson, 1990) in which the flow-producing appendages essentially stop during the sink phase of their swimming pattern. Since the nauplii are more dense than the water, during the period when the animal is not moving its appendages, it sinks. As the nauplius sinks, it rotates at a particular angular velocity to a stable orientation. The rate of reorientation depends on the distribution of mass in the animal and the hydrodynamic drag which arises from the relative motion of the animal and the surrounding fluid. Owing to the extension of the first antennae, calculating the hydrodynamic drag is quite complex for the adult. Nauplii, in contrast, have only rudimentary first antenna which are not considered to be important in the calculation of drag in this study. To determine the length of separation between the geometric center and the center of mass, the rate of reorientation to its stable position during the sink phase was measured. All measurements were made from digitized acetate tracings taken from pre-recorded video images of sinking copepods. The orientation angle from the vertical position was measured using NIH Image loaded on a Macintosh computer and the digitizing tablet, Mac Tablet.

### Orientation of *Acartia* nauplii entrained in a feeding current

Approximately 100 free-swimming *Acartia* nauplii were placed within the filming vessel containing the tethered *E. rimana*. The change in orientation, measured in degrees, of *A. hudsonica* nauplii when entrained within a feeding current was



**Fig. 3.** Orientation of *Acartia* nauplii prior to (A) and after (B) rotation by the feeding current of *E. rimana*. The final orientation (C) represents the prey's ability to escape in a direction different than its pre-escape orientation. Changes in orientation for positions A to B are measured from the predator's frame of reference, while the changes in orientation from positions B and C are measured from the prey's pre-escape orientation.



recorded using the video system and measured as described for the same organisms in still water.

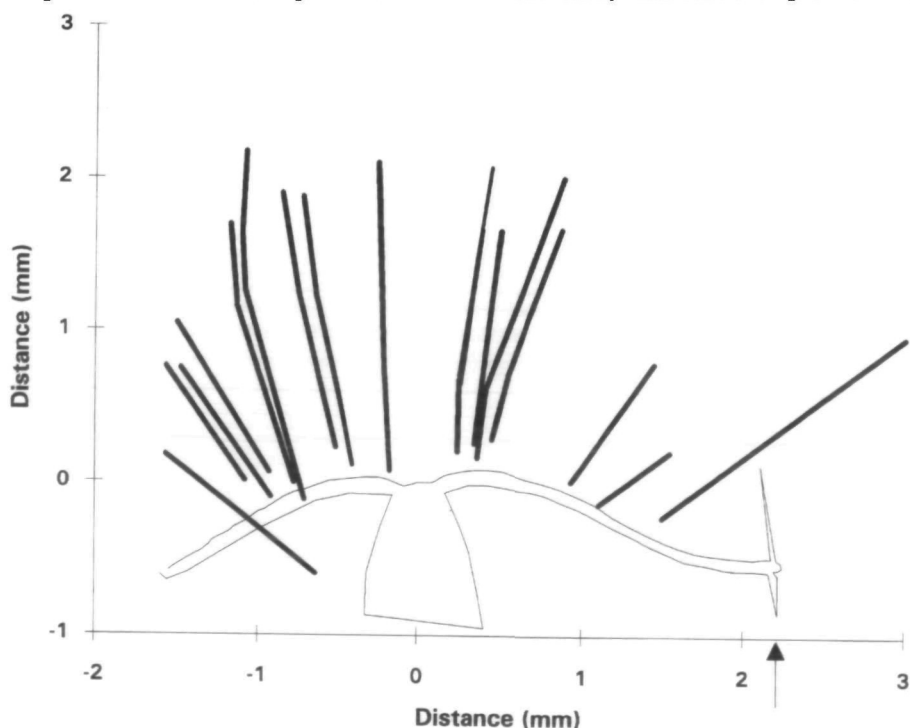
### *Escape direction of Acartia nauplii entrained in a feeding current*

The orientation angle of *Acartia nauplii* was measured for eight individuals one frame before and one frame after an escape response was elicited (Figure 3). By comparing the two measurements, the direction of escape was quantified as the change in the orientation of the body after the escape with reference to the prey's original orientation. The change in the angle measures the ability of the prey to exhibit a directional jump. A result of  $90^\circ$  would signify that the animal leaps at right angles to its pre-jump orientation, while a  $0^\circ$  result means the animal leaps directly forward.

## Results

### *Euchaeta feeding current*

For simplicity, only select particle trajectories, of the total 900 three-dimensional points recorded for the region above the first antennae of *E.rimana*, are shown in Figure 4. Since all the points tracked in this study traveled along a common



**Fig. 4.** Trajectories of select 20mm particles entrained in the feeding current of *E.rimana*. The spacing between points varies in time from 333 ms for the most distant points to 16.7 ms for the most proximal. The arrow on the X-axis represents the right distal tip of the antennae. The left distal tip is not shown in this graph.

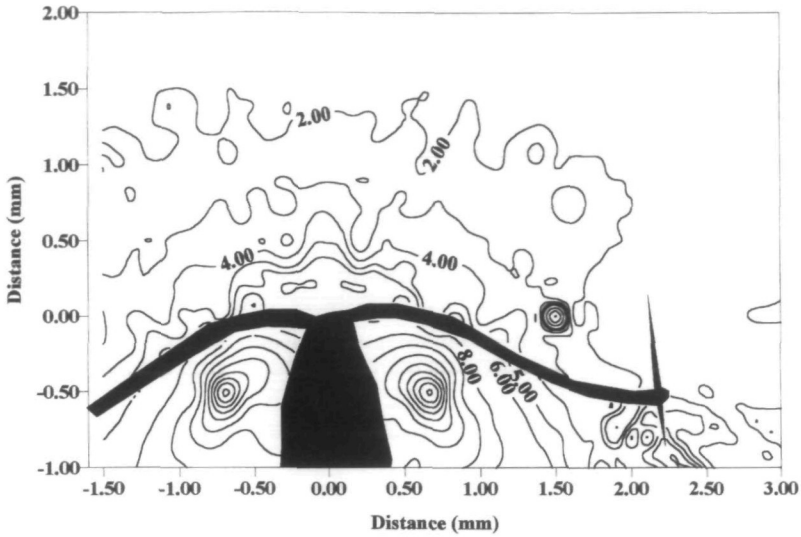


Fig. 5. Isolines of flow magnitude within the feeding current generated by a tethered *E. rimana*. The minimum contour is  $2 \text{ mm s}^{-1}$ . Contour intervals are  $1 \text{ mm s}^{-1}$  at speeds  $< 6 \text{ mm s}^{-1}$  and at intervals of  $2 \text{ mm s}^{-1}$  thereafter.

plane defined by the *YZ* coordinate, differences between the trajectories of the particles can be represented using only *XZ* coordinates. Contours of equal flow magnitude derived from the particle trajectories are shown in Figure 5. In general, the magnitude of the flow decreased with increased distance from the center of the head. The distal tips of the antennae were in water flow measuring  $1 \text{ mm s}^{-1}$ . This flow rate is  $\sim 10\%$  of the value found in the highest flow regions located above the first antennae. Figure 6 shows the magnitude of the feeding

#### Flow Speed Along the Antennae of *E. rimana*

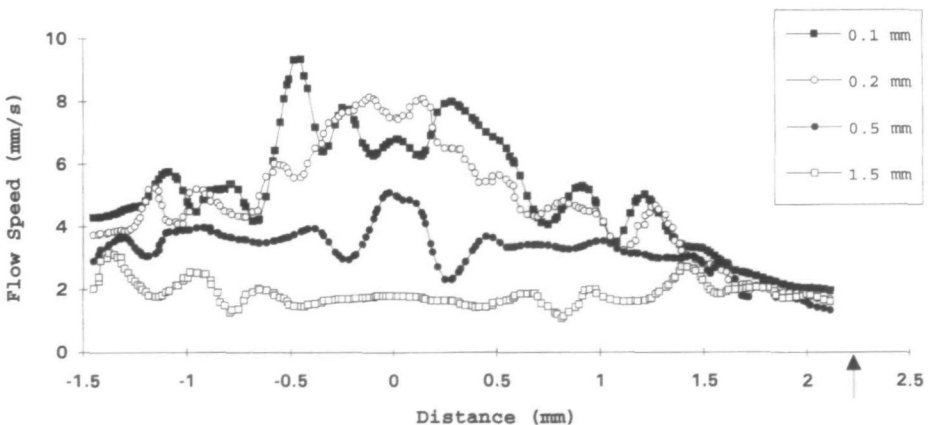


Fig. 6. Flow magnitude at several distances above the first antennae of *E. rimana*. Positive values represent the distance measured from the head along the right antenna of the animal.

current along profiles parallel to the antennae at varying distance above the antennae. At a distance of 1.5 mm above the antennae, the magnitude of the flow parallel to the antennae is fairly homogeneous at a speed of  $\sim 2 \text{ mm s}^{-1}$ . However, at a distance above the antennae between 1.5 and 0.20 mm, the profile shows a higher magnitude of water flow above the head and decreasing distally along the antennae. At a distance  $> 0.2 \text{ mm}$  above the antennae, the independent effects of the second antennae are minimal. However, closer to the antennae, 0.1 mm above them, the profile of the water flow reflects the motion of both appendages. Flow speeds were maximum above the first antennae at  $\sim 0.43 \text{ mm}$  from the head along the antennae, reaching values of  $\sim 10 \text{ mm s}^{-1}$ . Flow decreased both proximal and distal to this local maximum along the antennae.

The vorticity field for a portion of the feeding current of *E. rimana* is shown in Figure 7. Vorticity values ranged from  $0 \text{ s}^{-1}$  above the head of the animal to about a positive and negative  $10 \text{ s}^{-1}$  at  $\sim 1.7$  and  $1.0 \text{ mm}$  along the right and left antennae, respectively. A zero vorticity value in a moving fluid can result in two ways. The fluid rotation caused by the spatial variation in flow in the  $X$  direction can be equal in magnitude, but opposite in direction, to that caused by the variation in the  $Z$  direction. Alternatively, if there is no spatial variation in the velocity, there will be no vorticity. At the center of the feeding current, there is no variation in the flow velocity as a result of the left/right symmetry of the feeding current. This results in zero vorticity for this section of the feeding current of *E. rimana*.

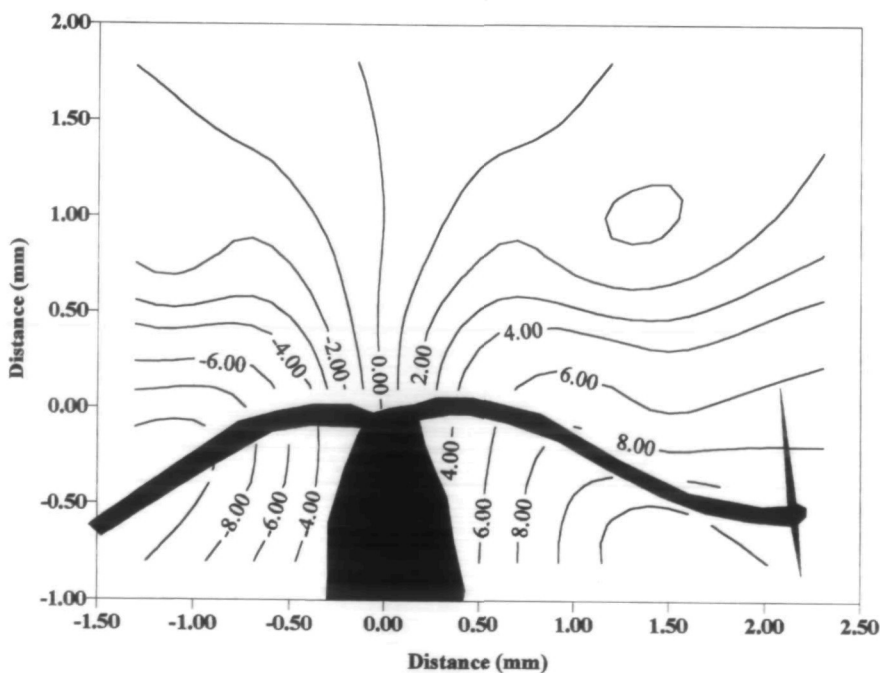


Fig. 7. Isolines of flows vorticity within the feeding current generated by a tethered *E. rimana*. The minimum contour is  $-10 \text{ s}^{-1}$ .



*Orientation of Acartia in still water*

Observations of *A.hudsonica* nauplii in still water show that the stable orientation is in the head-up position. When perturbed from this orientation during the 'hop' portion of its swimming motion, the rate of reorientation back to the stable orientation ( $d\theta/dt$ ) varies depending on the degree of perturbation and the distance separating the center of mass and the geometric center. The torque driving this rotation ( $T_g$ ) can be described numerically as:

$$T_g = L \times \sin \theta \times M \times g \quad (1)$$

where  $L$  is the distance separating the center of mass from the geometric center,  $\theta$  equals the radians of rotation from the vertical axis,  $M$  equals the mass of the object and  $g$  is the acceleration due to gravity. When immersed within a still viscous fluid, the torque required to rotate a sphere ( $T_v$ ) can be quantified as:

$$T_v = 8 \times \rho \times \mu \times r^3 \times \omega \quad (2)$$

where  $\rho$  is the density of seawater,  $\mu$  is the dynamic viscosity of seawater,  $r$  equals the radius of the organism (assumed to be a sphere) and  $\omega$  is the angular velocity of the organism (Jonsson *et al.*, 1991). If angular velocity is defined as  $d\theta/dt$ , then equations (1) and (2) can be combined and solved for the length of separation between the geometric center and the center of mass. Thus:

$$L = \left( \frac{6\mu}{\rho g t} \right) \int_{3\pi/4}^{\pi/4} \left( \frac{\delta\theta}{\sin \theta} \right) \quad (3)$$

The rate of reorientation of 20 individuals of various sizes ranging from 125 to 196  $\mu\text{m}$  was determined. From the rates of reorientation to the stable position, the average length of separation was calculated to be 0.27  $\mu\text{m}$  ( $\pm 0.04 \mu\text{m}$  SE).

*Orientation of Acartia nauplii entrained in a feeding current*

When a solid body is entrained within a sheared flow, as found in a copepod's feeding current, the assumed orientation is a balance of the acting rotational forces. Assuming a spherical body, the two forces are the torque due to the vorticity ( $T_t$ ) in the flow and, once rotated off the stable orientation, the torque due to the offset of the center of mass from the center of buoyancy [equation (2)]. The fluid-derived rotational force can be calculated as:

$$T_t = \frac{4}{3\pi} \times \mu \times r^3 \times \left( \frac{v}{2} - \omega \right) \quad (4)$$

where  $r$  equals the radius of the organism entrained within the flow,  $v$  is the vorticity of the flow and  $\omega$  is the angular velocity of the organism. Assuming that the nauplii are sinking through the water column in stable orientation prior to being entrained within the feeding current ( $\omega = 0$ ) and that any reorientation occurs without a lag period, equations (1) and (4) can be combined to predict

the instantaneous orientation of the nauplii at each point of its entrainment. The resulting equation is:

$$\theta = \sin^{-1} \left[ \frac{3\mu(\nabla v) \times (\rho_w)}{g \times L(\rho_a)} \right] \quad (5)$$

where  $\mu$  equals the dynamic viscosity of the water,  $\rho_w$  and  $\rho_a$  are the densities of the water and the animal, respectively, and  $L$  is the offset of the center of mass from the geometric center in terms of the radius of the sphere. The angle of orientation is, therefore, inversely related to the length of separation between the geometric center and the center of mass, and directly related to the magnitude of the vorticity. Assuming the length of separation remains constant over these short time frames, a stable orientation will be reached if the vorticity remains below a critical value such that  $\theta$  is not greater than  $\pi/2$ . For *A.hudsonica* nauplii, that critical vorticity was calculated to be  $0.1 \text{ s}^{-1}$ . At vorticity values greater than this, the nauplii will not reach a stable orientation, but rather will rotate at angular velocities approaching those characterized by the flow's vorticity. This is an important consideration for the region examined in this study because with the present combination of  $L$  for the prey and the flow vorticities found in the feeding current of this predator (Figure 7), the prey will spend most of its entrainment in rotation with the flow. Therefore, a predicted orientation of *Acartia* nauplii entrained within this flow must be calculated initially as a balance between the two sources of torque described above. Once within the critical vorticity region ( $V > 0.1 \text{ s}^{-1}$ ), a predicted orientation is calculated using the integrated vorticity value, calculated over discrete time frames. This value is then multiplied by the time the prey is entrained.

Because the vorticity values are spatially variable, each entrainment path will have a unique time-dependent vorticity pattern. For this reason, the predicted orientations for nauplii prey entrained in the flow are only reported for that position for which there were actual measured results. Eleven individual prey trajectories were mapped and are shown in Figure 8. Using the vorticity values found for *E.rimana*, the predicted orientations were calculated and are shown

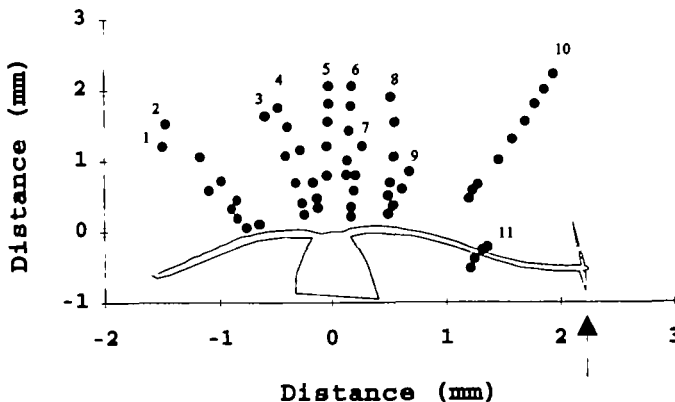


Fig. 8. Trajectories of *A.hudsonica* nauplii entrained within the feeding current of a tethered *E.rimana*. Path numbers are in reference to the final orientations listed in Table I.

**Table I.** Observed and predicted orientations of *A.hudsonica* nauplii entrained in different paths of the feeding current of *E.rimana*. Calculations for predicted orientations are described in the text

Path #	Size ( $\mu\text{m}$ )	Predicted orientation (degrees)	Observed orientation (degrees)
1	128	-58	-18
2	146	-18	-37
3	196	-29	-14
4	123	-37	-50
5	142	-11	-20
6	135	18	-20
7	176	29	-29
8	159	95	40
9	125	81	80
10	187	99	32
11	137	112	157

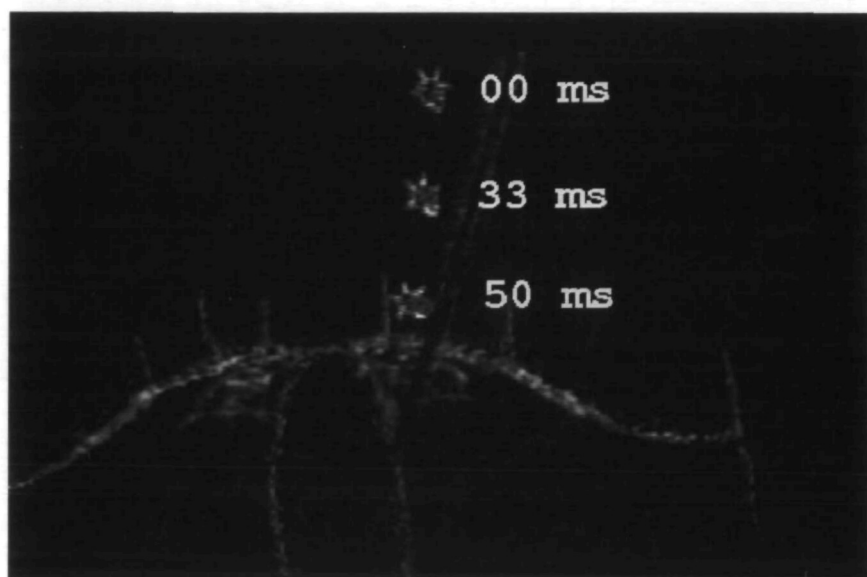
along with the actual measured angles of orientations in Table I for the final orientation for each of the 11 different paths. Angles are measured from the vertical with a counter-clockwise rotation giving a positive angle. In general, the predicted orientation of the entrained prey agreed reasonably well with the actual measured orientation. The observed orientations differed on average by  $33^\circ$  (SE  $7^\circ$ ;  $n = 11$ ) from the predicted orientations. Prey entrained from the left were rotated clockwise and those entrained from the right were rotated counter-clockwise. In both cases, the direction of rotation was towards the center of the feeding current. Figures 9 and 10A–C show the change in orientation of the prey as a result of being entrained within the feeding current.

#### *Escape direction of Acartia nauplii entrained in a feeding current*

When escaping, the nauplii did not simply leap forward, but rather they leaped at an average angle of  $\pm 10^\circ$  (SE  $0.7^\circ$ ;  $n = 8$ ) from their pre-escape orientation (their own frame of reference). Therefore, a prey, such as that described by track #7 (Table I), which was rotated to  $29^\circ$  from the vertical, will jump forward ( $\pm 10^\circ$ ) from its pre-escape position. This is equivalent to a net escape direction of  $19$ – $39^\circ$  from the vertical. Even with the ability of the prey to alter its escape direction, it will still leap towards the center of the feeding current. Figure 10C–E shows an example where the change in a prey's orientation as a result of the escape reaction was  $0^\circ$  from its pre-escape orientation.

## Discussion

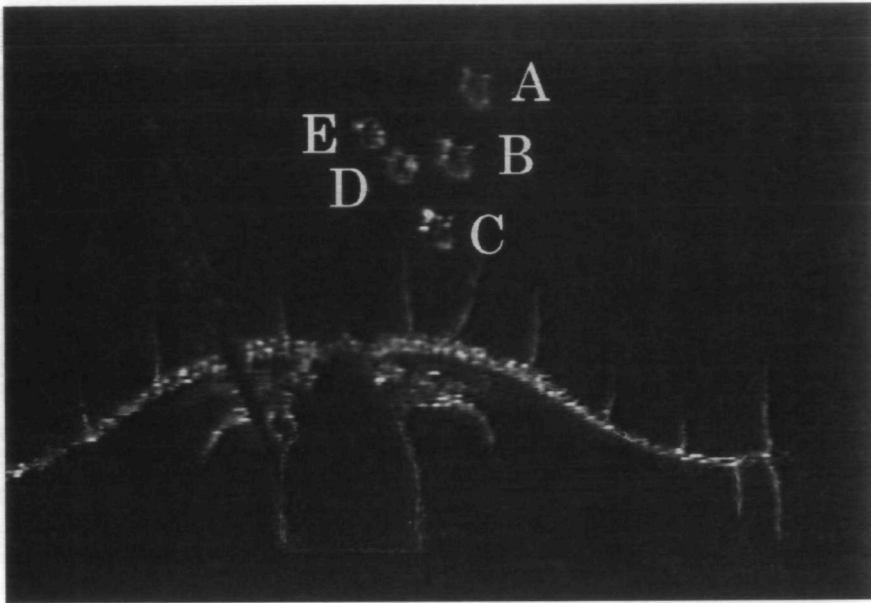
An important feature of planktonic calanoid copepods is their generated flow current. The flow serves the animals as a mechanism to move through the water column, avoid possible predators, and entrain potential food items towards its capture appendages. Recent literature has shown that the shape and magnitude of the flow field can have important repercussions on the ability of a



**Fig. 9.** Changes in the orientation of *A.hudsonica* nauplii as a result of being entrained within the feeding current of a tethered *E.rimana*. The entrainment path is the first three positions in path 9 shown in Figure 8. The angle of orientation, measured from the vertical, beginning with the most distant position, is 4, 31 and 63°, respectively.

copepod to conceal its location and identity from both its predators and prey (Fields and Yen, 1993). For instance, the size of the fluid mechanical disturbance created by the flow field of *Pleuromamma xiphius* is in excess of 175 times the actual volume of the animal's body. This large disturbance makes it quite perceivable to mechanoreceptive predators. When searching for prey, the shape of the flow field may aid certain copepods in capturing rheotactic prey by minimizing the detectability of the hydrodynamic disturbance (Strickler, 1985; Tiselius and Jonsson, 1990; Fields and Yen, 1993). By minimizing detection, the predator can delay the prey's escape reaction until it is within the capture region.

The importance of the feeding current on the predator-prey interactions of marine copepods has been indicated in the past (Tiselius and Jonsson, 1990; Yen and Fields, 1992; Fields and Yen, 1993). The literature suggests that prey detect their potential predators by the shear characteristics or the rate of fluid deformation of the feeding current created by the predator (Haury *et al.*, 1980; Kirk and Gilbert, 1988). Fields and Yen (1993) and Lenz and Yen (1993) add that it is the prey's own feeding current morphology which allows the detection of its predators by maintaining the distal tips of its antennae out of the rapid flow of its own feeding current. This study examined the interaction between the rotational characteristics of the predator's flow field and the morphology of the prey as it pertains to the orientation of the prey items entrained within this feeding current.



**Fig. 10.** Changes in the orientation of *A. hudsonica* nauplii when entrained within the feeding current of a tethered *E. rimana*. Changes in orientation in positions A–C are due to the feeding current of *E. rimana*. Positions C–E represent the change in orientation after the initiation of the escape reaction of *A. hudsonica*. Locations A–B are sequences separated by 333 ms, while the time elapsed between B and C is 234 ms. After the initiation of the escape, position D is 50 ms after C, while the orientation shown in E is 17 ms after D.

The discussion is divided into two aspects which deal with the interaction between the predator and prey. The first aspect considers the ability of the predator to maximize its capture success of the prey. The second portion will be in consideration of the prey, and its attempt both to detect its predator and escape predation.

#### *Maximizing predation rates*

*Acartia hudsonica* nauplii exhibit 'hop and sink' swimming behavior (Tiselius and Jonsson, 1990). During the 'hop' phase, the animal leaps forward 1–2 body lengths. After 'hopping', the organism stops its swimming appendage motion and begins to re-orient to its stable sinking orientation. Since the rate of re-orientation is quite rapid in still water, before they are entrained within a feeding current, *A. tonsa* nauplii have typically assumed their sinking orientation (personal observation). However, because the feeding currents of copepods are sheared and therefore contain local vorticity components within the flow (Yen *et al.*, 1991; Fields and Yen, 1993), the prey's orientation changes as it is entrained closer to the predator. This change in orientation is largely due to the continually changing balance of three interacting sources of torque (Figure 1).



One source of torque originates from the disparity in the location of the center of gravity and the geometric center of the animal. A second source of torque results from the flow in which the copepod is entrained. The rotational force from this source (measured as vorticity) is a result of the spatial gradient in flow velocities within the feeding current. As differential velocities strike different portions of the copepod's body, the animal is rotated towards the region of highest velocity. A third source of rotation is due to any asymmetry in the swimming motion of the entrained prey. Since *A.hudsonica* exhibit a 'hop and sink' swimming pattern, maintenance of a particular stable orientation through asymmetric swimming motion is not considered important. If the animal is not spherical, an additional source of torque is due to the rate of strain (Pedley and Kessler, 1987). This source of torque is not considered in this study. Therefore, by having a spatial variation in the flow velocity at a given radius from the source (a vorticity field), the predator essentially places a continual torsional force on the prey such that they orient toward the center of the feeding current. When an escape reaction is elicited by the prey, they will jump toward the center of the flow field ( $\pm 10^\circ$ ) rather than out of the flow field.

In a similar study, Kessler (1985) suggested that motile algal cells could be concentrated into a narrow beam if the flow vorticity was large enough to rotate the organism at an angle different from that due to the orientation derived from the center of gravity alone. However, for the cells to concentrate, the flow vorticity must not be so overwhelming as to cause the full rotation of the cells. In this latter case, full rotation will cause a portion of the cells to swim in a directed swimming as a result of the balance of gravitational and viscous forces is termed gyrotaxis. Gyrotaxis has been reported for dinoflagellates (Kessler, 1985) and modeled for smaller cells such as cryptophytes and *Chlamydomonas* (Mitchell *et al.*, 1990). Therefore in the language used by Kessler (1985), gyrotactic individuals such as those used in this study would tend to be 'focused' towards the center of the feeding current. The concentration of prey would occur even in high-vorticity regions if the time entrained within the highly sheared region of the feeding current was short enough that rotation over  $180^\circ$  did not occur. Although only the dorsal view of the vorticity field is presented in this study, the three-dimensional feeding current data from Fields and Yen (1993) suggest that the tendency for orienting the prey towards the center of the flow field should be true for the entire volume above the first antennae of the predator due to the funnel shape (albeit asymmetrical) of the entire feeding current.

In rotating the prey, the predator's feeding current changes the orientation of the prey's first antennae relative to the streamlines of the feeding current. Since streamlines converge with decreasing distance from the predator, the differences in flow speed, measured perpendicular to the streamlines at a distance covered by the span of the prey sensors, also increase (Yen and Fields, 1992). If the sensors are not oriented perpendicular to the streamlines, the relative differences in velocity measured at the distal tips of the antennae are quite different than if they had remained perpendicular (Haury *et al.*, 1980). This variation in sensor orientation may help explain the high variability in shear values calculated by Yen and Fields (1992) for these same prey entrained within the feeding current

of *Temora longicornis* and for *Calanus finmarchicus* escaping from a stationary object (Haury *et al.*, 1980).

#### *Predation avoidance by Acartia sp.*

*Acartia* sp. are typically the most numerically abundant copepod found in many coastal regions. The ecological success of this copepod genus often relies on a precarious balance between its reproductive rates and its aptitude at predator avoidance. Historically, much attention has been dedicated to the abilities of *A. tonsa* to reproduce and indeed this rate is astounding for an organism this large. Population biomass doubling times have been reported to achieve values up to one doubling per day (Durbin and Durbin, 1981). However, predator avoidance may also add to the success of this genus. During the summer in Chesapeake Bay, USA, invertebrate predators can consume up to 78% of the population per day (Purcell, 1992). With such intense predation pressure, it is probable that the animals have evolved mechanisms to maximize their ability to avoid predation. One aspect of predator avoidance is the ability to detect the location of a potential predator and then elicit a rapid escape response. A second means for prey to minimize predation is by maintaining their orientation relative to their predators in a manner which is favorable for successful escape.

Mechanoreception at the distal tips of the prey's antennae has been suggested as the probable location for predator detection (Yen and Fields, 1992). Neurophysiological data showing much neural activity associated with the stimulation of the distal tips (Yen *et al.*, 1992; Lenz and Yen, 1993) and the extension of the distal tips of the antennae into relatively quiescent waters (Fields and Yen, 1993) add credence to this hypothesis. However, an additional method for predator detection may be associated with the increasing rate of inclination caused by the entrainment of the prey into a predator's vorticity field. When a prey item is entrained within a feeding current and begins to rotate, a different flow velocity will be felt on either side of its body, indicating to the prey that it is entrained within a given vorticity field. In addition, because the location of the predator is highly predictable from the direction of the rotation (always towards the region of most rapid water flow), a fairly accurate three-dimensional location of the source of the flow could also be possible. If the prey uses the rate of inclination as a mechanism for predator detection, the sensitivity of the system will depend on the degree of separation between the geometrical center and the center of mass of the prey. The smaller the separation, the more sensitive the animal will be to spatial variations within the flow velocity. Prey with very small separations between the geometric center and center of mass, however, will be prone to continual rotation when entrained within high-vorticity fields. This may make the direction of the prey escape unpredictable by the predator. In contrast, large separations may maintain the prey in a relatively vertical orientation. Although predator detection by monitoring the rate of change in the angle of inclination would be less sensitive, once the prey escapes, it would not be continually focused towards the center of the feeding current of its predator.

The separation of the geometric center and the center of mass found in this study was considerably smaller than has been assumed in the past. Kessler (1985) suggested that for the dinoflagellate *Dunaliella*, the length of separation ranges from 1 to 5% of the cell's radius. He assumed 3% for his calculations. Jonsson *et al.* (1991), however, found the length of separation for the bivalve larva *Cerastoderma edule* to be  $\sim 1 \mu\text{m}$  or 0.7% of its radius. This study found the length of separation in *Acartia* nauplii to be 0.4% of its radius. With such a small separation, the prey are more susceptible to rotation in smaller spatial velocity gradients than the past literature would suggest. Therefore, when confronted with a flow-producing predator such as *E.rimana*, *A.hudsonica* has little ability to maintain its upright orientation. Consequently, control of the prey's orientation becomes dominated by the characteristics of the predator's feeding current. This observation suggests the importance of the predator's feeding current in its ability to orient and subsequently capture specific prey. The instantaneous orientation of the prey resulting from its interaction with the feeding current of the predator may be quite species specific, depending on both the predator and the prey. Variation in feeding currents between individual predators and, more importantly, between different genera, may give rise to the ability of different predators to capture different prey. In addition, different species may vary in their degree of separation between the geometric center and the center of mass and, within a given species of prey, the relative separation may vary with ontogeny. The variation with ontogeny, in conjunction with the increased swimming ability of the higher age classes, may make these animals less vulnerable to predation and help explain the upper limit in the size-selective predation documented for a particular species (J. Yen, unpublished).

While the possibility of decreased predation may be facilitated by being strongly geotactic, the decreased ability of the prey to assume a bearing different from being in line with the force of gravity may give an evolutionary constraint to the maximum separation between the location of the center of mass and the geometric center. Thus, there may be a trade-off between the ability of the prey to orient itself using its own swimming abilities and the increased predation which results from its orientation being determined by the feeding current of its predators. The success of an attack of a predator, or the escape of a prey, may be highly dependent on the relative spatial orientation of the predator and prey. Further understanding of the dynamics of planktonic populations requires observations at the location and on the scale that predators and prey interact in nature.

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