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Escape responses of *Acartia budsonica* (Copepoda) nauplii from the flow field of *Temora longicornis* (Copepoda)

By J. YEN and D. M. FIELDS

With 7 figures and 1 table in the text

Abstract

Three dimensional visualization of escapes of *Acartia budsonica* nauplii (250 μm) from the flow field created by a predator (the copepod *Temora longicornis*) permitted analyses of hydrodynamic cues at temporal and spatial scales that are biologically relevant to these plankton. Within a narrow corridor above the predator's primary sensors, the first antennae, the points of escape by the nauplii were mapped. The velocity of the nauplius at the point of escape was compared to the velocity gradient of the flow field. We found large variability in a) the average acceleration of $0.53 \text{ mm/s}^2 \pm 120.5\%$ (coef. var.), computed along the streamline over a time interval corresponding to a distance travelled of one body length, b) the average shear of $0.80/s \pm 84.5\%$, computed perpendicular to the streamline over a distance equivalent to the span of the sensor, and c) the average relative velocity, where the velocity of the nauplius was $0.74 \pm 27.1\%$ that of the surrounding water. The best predictor of the point of escape was the relative velocity, the measured parameter that was least variable. The difference in the movement of the water and that of the nauplius could generate the necessary setal bend to trigger the escape response. To avoid predation, nauplii should rely on a cue that minimizes the risk of capture. Since most distant escapes occurred where velocity contours were curved (high shear), shear was considered the cue to alert nauplii to the presence of the predator. Distance to the predator and velocity of the nauplius were not considered potential cues because 1) distance cannot be perceived nonvisually, and 2) within a temporally-constant and spatially-uniform velocity gradient, the movement of the nauplii follows that of the water; constant velocity causes no setal bending which is necessary for the perception of water movement.

Introduction

Zooplankton exhibit escape reactions from predators and they also try to escape from towed instrumentation, such as those described here in this workshop on Advanced Techniques for in situ Studies of Zooplankton Abundance, Distribution, and Behavior. What signals elicit such escape reactions in a mechanoreceptive aquatic organism? To fully understand this interaction, we must characterize the sensors and sensitivity of the prey and the signals generated by the predator. Here, we examine the interaction between the naupliar stage of a copepod prey and an adult copepod predator.

Copepods have sensors that detect variations in light, chemical gradients, and mechanical stimuli. Visual perception is limited to variations in light levels as most copepods have simple photoreceptors, and therefore are unable to form images (LOWE 1935, ELOFSSON 1971). Copepod chemoreceptors are sensitive to pheromones (GRIFFITHS & FROST 1976) or plankton exudates (POULET & MARSDEN 1978, FOUR & GOLDMANN 1981, BUSKEY 1984). Possible chemo-

sensitive receptors such as aesthetascs (FRIEDMAN 1980) and pores (FLEMING 1973, MAUCLINE et al. 1977) are found on copepod antennae and mouthparts as well as over other areas of their cuticle. Mechanoreceptors are sensitive to water movements. The feathery and many of the setae on the antennae of copepods are the suspected mechanoreceptors (STRICKLER & BAL 1973, BARRIENTOS 1980, GILL 1986). According to HAURY et al. (1980), the first antennae are good sensors for detecting spatial differences in the flow regime. Since they extend out from the copepod's body, they are able to sample flow in a regime different from that of the body. The orientation of the sensory setae in the flow indicates that they are strategically positioned to intersect flow in three orthogonal planes (YEN & NICOLL 1990). From electrophysiological studies (YEN et al. 1992), long setae found at the distal tip of the first antennae appear sensitive to mechanical displacement, either of the surrounding water or of the seta itself where the rate of change in mechanical displacement of the sensor releases the neural response.

Hydrodynamic signals generated by aquatic predators can be found in their flow field. Copepods generate flow fields in order to bring water and entrained prey to the sensors and mouth. This flow field can also move the copepod through water or, when balanced with gravity, maintain its position in the water column (STRICKLER 1982, YEN et al. 1991). Within this flow field, a velocity gradient is created. Knowledge of the magnitude and shape of the velocity gradient permits calculations of acceleration and shear. Recent work (SINGARAH 1975, HAURY et al. 1980, ZARET & KERFOOT 1980, KIRK & GILBERT 1988, WILLIAMSON & VANDERFLOEG 1988, TISELIUS & JONSSON 1990) indicates that neither a specific threshold flow velocity nor acceleration triggers the escape response in ciliates (TISELIUS & JONSSON 1990) or rotifers (KIRK & GILBERT 1988). TISELIUS & JONSSON (1990) comment that, 'The faster the flow is, the farther away will a prey detect the copepod'. However, they found that there was no consistent threshold velocity that stimulated the escape of the ciliates in their study. HAURY et al. (1980) suggest that fluid deformation or deformation rate should cause the escape response. However, they were not able to demonstrate this.

Here, we determined the coordinates at the point in space (x, y, z) and time (t) where copepod nauplii (*Acartia hudsonica*) escape from the flow field created by the omnivorous copepod *Temora longicornis*. By computing the values for fluid and naupliar velocity, acceleration, and shear at the (x, y, z, t) points of escape, we develop methods to quantify hydrodynamic signals that could stimulate a mechanoreceptive response. These flow characteristics were computed over temporal and spatial scales that are biologically relevant to the prey. In addition, we sought to identify the variable that was the best predictor of when the nauplius will initiate an escape from a predator.

Materials and methods

Zooplankton collection

Copepods were collected from Sony Brook Harbor, NY, during April and May 1991. Adult *Temora longicornis* and *Acartia hudsonica* females were selected from these tows. The *A. hudsonica* were placed in containers with sea water (15 °C) and phytoplankton (*Thalassiosira weissflogii*) to stimulate egg production and subsequent naupliar growth. From these cultures, we selected nauplii of *A. hudsonica* which then were transferred through a filtered sea water rinse.

After acclimation to room temperature, several *T. longicornis* were glued to hairs a few hours prior to the experiment. We selected the copepod with the best-positioned tether that exhibited the most con-

tinuous beating of its second maxillae. For this analysis, only one *T. longicornis* was used to generate the flow field. For two hours, the behavior of the tethered *T. longicornis* was monitored in the presence of 20 μm polystyrene spheres (PolySciences) to map the hydrodynamic structure of the flow field. For two additional hours, 500 *A. hudsonica* nauplii (250 μm) were added and their escape behavior monitored.

Video-imaging

In order to examine these prey-predator interactions of copepods, we duplicated the same technology of fixed-frame laser-illuminated video-imaging of STRICKLER (1985). Filming was done using a single HeNe laser (632.8 nm) light source with a split beam projected onto two perpendicular facing cameras. In this way, simultaneous $x-z$ and $y-z$ views of the copepod were obtained. All direct light to the cameras was blocked and only diffracted light was recorded. The laser light did not appear to be detected by the copepods. The tethered copepod was placed in a small (100 ml) tank and positioned at the focal points of both cameras. The tank had been filled with sea water that had been filtered through a 0.45 μm glass fiber filter to remove extraneous particles that interfere with the optical pathway between the laser light source and the video camera. The two tapes were analysed individually. A brief flash of a strobe light synchronized the two videos of the two views of the copepod interactions. The speed of the video recording was 30 frames per second.

Flow field analysis

To minimize the complication of three dimensional analysis, a narrow corridor above the predator's first antennae and along the entire length of the antennae was mapped by following the pathlines taken by the 20 μm polystyrene spheres caught in the flow within that narrow corridor. However, it was necessary to utilize three-dimensional viewing to identify particles within this corridor: from the $y-z$ view of the flow field, those particles that remained within the narrow corridor were identified as the same particles observed in the $x-z$ view. Only these particles were followed in the $x-z$ view to map their trajectory. The region (3.5 mm across by 1.9 mm) above the first antennae was chosen because these appendages carry the most sensors for prey detection. The sides of the corridor that enclose the two dimensional view were 280 μm in front of and 280 μm behind the plane of the first antenna which accounts for less than one body width of the animal (Fig. 1). By assigning the three-dimensional origin to the top of the head

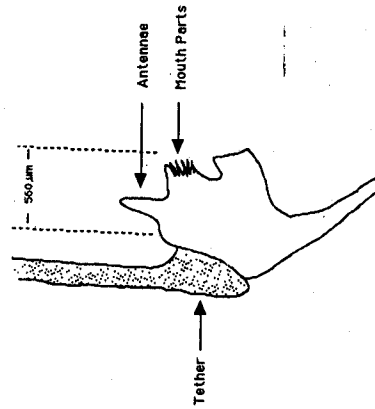


Fig. 1. Profile of the copepod, *Temora longicornis*, tethered to a hair, illustrating the narrow corridor (560 μm in width) within which particles and nauplii caught in the flow were followed for the three dimensional analysis of the flow field.

of the tethered animal, cartesian coordinates for x , z and y , z positions for individual particles were determined from each of the cameras respectively. The velocity (dx/dt) of the particle and hence fluid was calculated as distance (x) travelled over a specified time interval (t) where distance was calibrated by filming a portion of a millimeter ruler at the same position as the animal. The velocity contour map was constructed by analysis of the x , z position and the velocity at those coordinates using a contouring software package (SURFER) and a 386-33 Hz Gateway 2000 microcomputer.

Kinematics of prey-predator interactions

Prey escape trajectories were drawn by plotting the position of the nauplius relative to the predator in frame-by-frame analysis. The (x , y , z) position at which the escape was elicited was determined. The O, O, O point was designated as the tip of the prosome of the copepod at the midline of the plane of the antenna. Since only escapes that occurred within the 0.56 mm corridor were used, a value of O was used as the y -coordinate. Three-dimensional coordinates were assigned to the location of the initial and multiple escape responses of the *A. hystorica* nauplii ($n = 20$ different nauplii).

Fluid velocity was determined at each escape location by plotting the coordinates of the escape responses directly onto the flow field velocity contour map. Actual prey velocities at which the escape responses were initiated were computed from the distance travelled by the nauplius over the 1/6 sec (5 frames) just prior to the initiation of the escape response.

The relative velocity was calculated as the ratio of the velocity of the nauplius at the point of escape and the velocity of the particles caught at that very position in the flow field. These velocities were not determined simultaneously; the velocities of the particles were determined within a ten minute interval which is less than 5% of the total 4-hour time interval examined while the velocities of the nauplii were taken over a two-hour interval after these quasi-instantaneous flow velocities were determined. Since the velocities of the nauplii were determined later than when the water velocity was determined, there could have been a steady change in the gradient over time. Analysis of the change in the relative velocity (V_r/V_w) over time showed no sequential decline or increase. Therefore, the flow field was stable over the four-hour time interval examined in this study.

Acceleration is the change in velocity over time (dv/dt). We chose a time interval of 1/6 sec. On average, the distance travelled during this time interval was approximately one body length or 250 μ m. Acceleration was computed from the trajectory of prey entrained in the flow field for two 1/6 sec intervals just prior to the naupliar escape.

To estimate shear (dv/dx), the change in velocity over a designated distance is computed. We chose the 250 μ m span of the antennae of the nauplius, an important sensor. Sensor orientation was assumed to be perpendicular to the fluid motion of the flow field generated by the tethered animal. Hence, shear was calculated perpendicular to the streamline.

Signal to escape

It is difficult to assign a cause and effect relationship between a stimulus and a behavioral observation if the underlying sensory mechanism is not fully understood. However, the ability of a defined stimulus to elicit a predictable behavior pattern does lend credence to a possible causal relationship and makes the stimulus a valuable predictive tool. In this paper, we suggest that the stimulus with the lowest coefficient of variation (CV) for eliciting an escape response is the most valuable predictor.

The CV of the relative velocity of the copepod nauplius to the surrounding fluid was calculated by first determining the ratio of the paired velocity measurements. Each velocity measurement was made on an individual at a particular time and point where the 20 individuals reported act as replicates of the escape response. Therefore, since we were interested in the variability of the ratio between individuals and not the variability of the ratio itself, we calculated the CV of the 20 ratios treating each as an individual replicate. The inherent variability in the ratio due to errors in our precision were not addressed in this CV. That variability however was presumably consistent in all our other calculations, making the comparison between paired velocity measurements, treating each pair as a replicate. Hence, the coefficient of variation represented the variability in relative velocity, acceleration, and shear.

Results

The experimental set-up involved the use of a tethered copepod in the center of the field of view of two cameras oriented at right angles to each other. Two right-angle views provided the information to get the three-dimensional position of the velocity as well as the point where the nauplius initiated its escape. Although tethering may produce some inaccuracies in the natural flow field structure around *T. longicornis*, the tethered animal was used only to create a velocity gradient. We then presented this velocity gradient as a source of hydrodynamic disturbance from which the nauplii escape. We were not examining the specific traits of the flow field for this particular copepod.

Quantifying the hydrodynamic signal that triggers the escape of a prey from a predator demands accuracy in the location, in time and space, and the magnitude of a) the hydrodynamic signal within the velocity gradient surrounding the copepod and b) the velocities of the nauplii just prior to their escape. This analysis also requires a careful understanding of the temporal and spatial scales by which these signals act on these animals. Our approach to this quantitative analysis was as follows:

Flow field

To get a true representation of the velocities within the flow field, we must use three-dimensional information of the position of the particles that follow the pathlines of the flow. To simplify the task without losing accuracy, we analysed only a narrow corridor through the flow field. Within this thin planar slice, we measured the three-dimensional velocities of the particles following the flow as well as the nauplii caught in the flow, but only of those particles and nauplii that were within this plane. Thus, we could answer our question and illustrate the

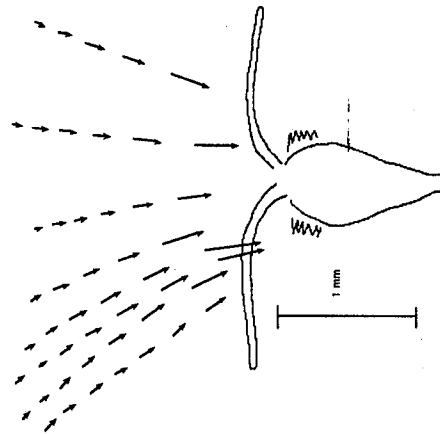


Fig. 2. Illustration of the flow field (3.5 mm across by 1.9 mm) representing the velocity gradient within the 560 μ m corridor above the first antennae of *Temora longicornis*. Each arrow represents 1/6 sec of travel. The eight streamlines were mapped from a total of 98 data points.

results in a simpler two dimensional picture rather than in three dimensions. Continuing research using this same analytical procedure to map the position of escapes within the entire three-dimensional flow field will examine how the points of escape vary with respect to the location of the sensors, mouth, or velocity gradient.

We found that, in the region above the first antennae, flow velocities varied from zero to over 2 mm/sec near the antenna (Fig. 2). The parallel streamlines indicated laminar flow, and the field was funnel-shaped. Although only 8 particles were followed (with 98 point velocities taken), the steadiness in the laminar flow permitted extrapolation of velocities between flow lines. Without a flow field, the settling velocity of the particles was 0.15 mm/s.

Within this framework, there was still a component of variability in these velocity measurements because we assumed that any particle that passed through this corridor followed a pathline that was parallel to the sides of the corridor. If the particle actually followed a diagonal path from the top of the 1.9 mm corridor through the 0.56 mm wide corridor (length of the diagonal = 1.98 mm), then there could have been up to a 4.3% overestimate in velocity.

Velocity contours

The contours were relatively flat in the middle of the field and curved at the edges (Fig. 3). Highest velocities were found at the base of the funnel-shaped flow field near the antennae.

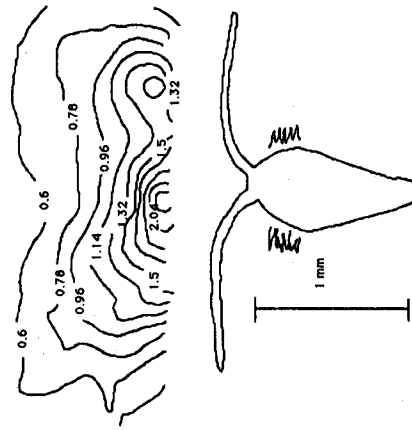


Fig. 3. Contour map of equal velocity constructed from the flow field within the corridor above the first antennae of *Temora longicornis*. Velocities reached 2 mm/s at a distance of 0.5 mm above the tip of the prosome.

Points of escape

Only nauplii from a single species of copepod (*A. hudsonica*) and only of a single size (250 μ m) were used to minimize the variability due to different expressions of the genotypes or phenotypes of the group of animals under examination. Escape distances of these nauplii from the copepod varied from 0.80 to 2.22 mm (Fig. 4, Table 1). A representative prey trajectory (Fig. 5) illustrates the escape behavior where there were multiple jumps of the nauplius. Prey,

Table 1. Characteristics of the flow field of *Temora longicornis* at the points where nauplii of *Acartia hudsonica* initiate their first escapes. At each point of escape, the (x, z; y = 0) coordinates, the distance from the tip of the prosome (0, 0, 0) of *Temora longicornis*, the velocity of the water and the nauplius, the relative velocity of the nauplius vs water, the value of the acceleration of the nauplius over 1/6 sec along the streamline, and the value of the shear of the water across the span of the naupliar sensor perpendicular to the streamlines are given. Note that the coefficient of variation (CV) is lowest for the value of the relative velocity (V_n/V_w).

Location		Distance (mm)	¹ Water Velocity V_w (mm/s)	² Nauplius Velocity V_n (mm/s)	V_n/V_w	³ Nauplius Acceleration (mm/s ²)	³ Shear (1/s)	
X	Z							
-1.16	1.05	1.56	0.93	0.72	0.77	0.00	0.68	
-0.96	1.25	1.58	0.93	0.60	0.65	0.00	0.40	
-0.62	0.78	1.01	1.56	0.48	0.31	-0.36	0.88	
0.91	1.23	1.53	0.89	0.84	0.94	0.00	0.20	
-1.28	0.83	1.53	0.84	0.96	1.14	0.00	1.20	
0.54	1.43	1.53	0.75	0.94	1.24	0.00	0.20	
0.73	0.95	1.20	1.22	0.96	0.79	0.36	0.20	
1.13	1.57	1.93	0.60	—	—	—	—	
0.60	1.01	1.17	1.14	0.78	0.68	1.44	0.40	
-1.21	0.61	1.36	0.79	0.54	0.68	1.08	1.72	
0.42	0.87	0.97	1.20	0.78	0.65	-0.36	0.88	
0.92	0.72	1.17	1.15	0.66	0.57	0.72	1.92	
0.89	0.58	1.06	1.06	1.02	0.96	1.18	2.60	
-0.34	0.72	0.80	1.87	1.02	0.55	0.72	0.80	
0.35	0.88	0.95	1.13	0.90	0.80	1.44	0.68	
-0.62	1.10	1.26	1.18	0.66	0.56	0.00	0.60	
0.89	0.96	1.31	1.06	0.90	0.85	0.00	0.36	
0.74	1.12	1.34	0.97	0.54	0.56	0.00	0.12	
0.98	1.02	1.41	0.92	0.90	0.98	1.08	0.52	
-1.93	1.09	2.22	0.61	0.60	0.98	0.72	—	
Mean							0.74	0.53
Variance							0.04	0.45
CV							27.05	84.45

¹ Velocity (dx/dt) based on particle motion.

² Velocity (dx/dt) and acceleration (dV/dt) based on actual prey motion.

³ Shear (dV/dx) values calculated using $dx = 250 \mu$ m based on length of prey 1st antennae.

caught in the flow field, were drawn toward the predator along the streamlines of the flow field. Prey escapes were at an angle from the streamlines. Unless the prey exhibited a high speed jump that removed the prey completely from the influence of the flow, it was repeatedly drawn into the flow by ineffectual escapes. At this point, it could be captured or it could become akinetic and follow the streamline. Prey, which are akinetic and do not generate hydrodynamic signals, do not appear to be sensed by mechanoreceptive predators (Yen pers. obs.). Thus, if the streamline does not direct the nauplius to the copepod's mouth, the nauplius should successfully elude capture.

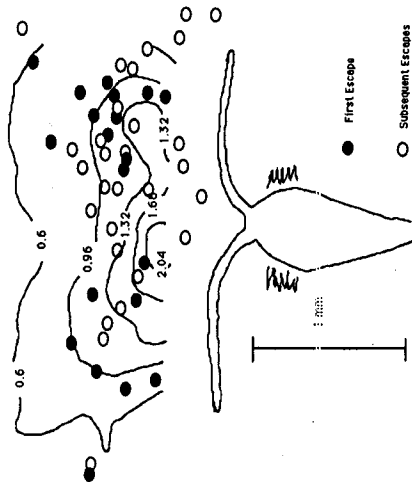


Fig. 4. Positions within the corridor above the first antennae of *Temora longicornis* of the points of escape exhibited by the nauplii (250 μm) of *Acartia hudsonica* relative to the velocity contours (mm/s). Solid circles represent the first escapes ($n = 20$) while open circles represent subsequent escapes ($n = 29$). Note how close some of the nauplii got to the central region of the flow field above the first antennae, while in the region where the velocity contours are curved, escapes are executed farther away from the copepod.

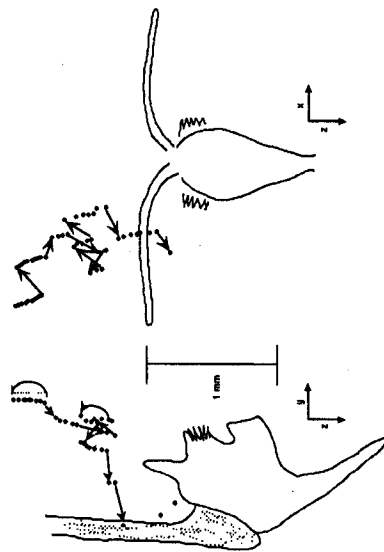


Fig. 5. Trajectory of a nauplius of *Acartia hudsonica* that became entrained within the flow field of *Temora longicornis* and tried to escape several times. The view from one camera gave the x , z positions and the view from the other camera gave the y , z positions. Cameras were oriented at right angles to each other. Each dot followed the movement of the nauplii 1/6 s apart while arrows depicting jumps were 1/30 s apart. Tiny dots illustrated a jump back to original position.

Relative velocity

At their points of escape, the velocities of the nauplii varied between 0.48 to 1.02 mm/s (Table 1). The velocities of the water varied between 0.60 to 1.87 mm/s. The average relative velocity of the *A. hudsonica* nauplii was $0.74 \pm 27.1\%$ (coef. variation) that of the surrounding water. The range of these values was between 0.31 to 1.14.

Acceleration

In order to calculate acceleration, a temporal scale for the change in velocity must be chosen. It is important to base this choice on some biologically relevant parameter. Ideally, acceleration of the nauplius should be calculated over a time interval equivalent to the reaction time of the sensor on the escaping prey. That is not well-known. Until further results of neurophysiological and behavioral research can provide the difference in time between the application of the stimulus and the time that a behavioral response is elicited, we decided to use a time scale corresponding to a distance travelled of one body length. Acceleration of the prey caught in the flow, calculated along the streamlines, showed wide variations between -0.36 to $+1.44$ mm/s^2 , with an average of $0.53 \text{ mm/s}^2 \pm 120.5\%$ (coef. variation; Table 1). Some escapes occurred close to the mouth where acceleration was high. This variability could be related to the beat frequency of the second antennae where the powerstroke vs recovery stroke produce rhythmic changes in acceleration. However, this is not the case here since acceleration was calculated over time intervals greater than the beat frequency, precluding discernment of any pulses occurring over smaller frequencies.

Shear

Where velocity contours were curved, the change in velocity over distance, or shear, was high; for example, above the distal tips of the antennae. Many escapes occurred in this region. In order to calculate the shear experienced by the nauplius, a spatial scale for the change in velocity must be chosen. To be biologically meaningful, the span of the mechanoreceptive sensor array was chosen as an appropriate length scale for this calculation. Shear, calculated as the distance between left and right antennal setae of a nauplius (250 μm) within the space perpendicular to the direction of the streamline (Fig. 6), was quite variable (Table 1), ranging between 0.12 to 2.60/s with an average of $0.80/\text{s} \pm 84.5\%$ (coef. variation). Variability could be introduced into the shear estimates since the orientation of the sensors may not necessarily be perpendicular to the streamlines, as assumed here, and requires further analyses.

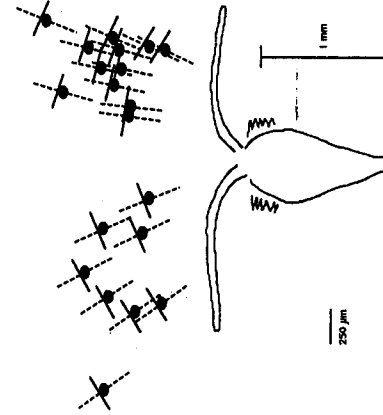


Fig. 6. Illustration of the model used to compute shear of the nauplii at their points of escape over a span (250 μm) of their sensors on a plane perpendicular (solid line) to the streamlines. Dotted lines were drawn parallel through the streamlines.

Discussion and conclusions

The escape reaction of prey from predators is a critical response for survival; an error here could cost the nauplius its life. Zooplankton avoidance of towed instruments is a practical consideration for improvements of the accuracy of their measurements. By duplicating and using the techniques in video-imaging developed by STRICKLER (1985), we examined the signals within water motion that appear to trigger the escapes of zooplankton. We describe a method to examine escape reactions of plankton. We discuss the considerations for the quantitative analysis that were necessary in our attempt to identify the hydrodynamic cues that elicited escapes of mechanoreceptive prey from the flow field of a predator.

Assuming equally precise measurements of fluid vs. naupliar velocities, similar nauplii and temporal stability of the predator's flow field, we found that there was a high degree of variability in the values of relative velocity, acceleration, and shear at the points of escape of the nauplii. All the escapes we viewed occurred at water velocities between 0.60 and 1.87 mm/s. The best predictor of the point of escape was the relative velocity which showed the lowest amount of variability. On average, the *A. hudsonica* nauplius escape response appears to be elicited when its own velocity is 74% ($\pm 27.1\%$ C.V.) that of the surrounding water. The nauplius seems to lag behind the velocity of the fluid at their points of escape.

How does a zooplankton sense the presence of the predator enveloped within these velocity gradients? Because most copepods lack well-developed eyes, it is unlikely that they can assess their distance from another predator or prey, visually. Electrophysiological studies (YEN et al. 1992) show that neural impulses are elicited whenever the setae are bent and there appear to be different sensitivities to bending in different directions. When the fluid is moving faster than the nauplius body, the setae, which follow the fluid movement, are bent relative to the body which lags in the fluid. The inertial mass of the nauplius, as it adjusts to the new velocity, may cause this velocity difference or slippage of the nauplius relative to the water. Slippage is the integrated effect of shear operating on the whole animal. In a spatially uniform accelerating field (Fig. 7B), both setae on either side of the nauplius may bend symmetrically, while in a shear field (Fig. 7C), the setae may bend asymmetrically. However, in a temporally-constant and spatially-uniform velocity field (Fig. 7A), the velocity of the nauplius and the setae synchronously follow the water movement so there is no setal bending and hence, no sensory

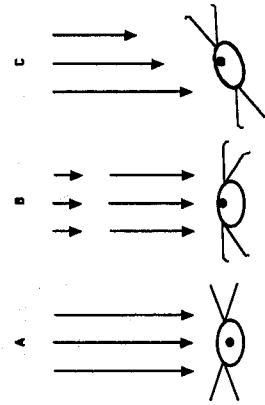


Fig. 7. Three simple velocity gradients to illustrate how a nauplius perceives water movement by setal bends. A) Temporally-constant and spatially-uniform velocity field where the nauplius and setae follow the flow with no setal bending, and hence no sensory input. B) Spatially-uniform acceleration field where setae follow flow while nauplius lags behind, resulting in symmetrical setal bends. C) Shear gradient in flow where setae follow water flow while nauplius lags behind, resulting in asymmetrical setal bends.

input. From this discussion, we conclude that both acceleration and shear should be detectable where shear may also give information on direction. To confirm the identity of the hydrodynamic stimulus that releases the escape response, experiments must be designed where various flow parameters are changed relative to each other (e.g. TURTZ 1979). Once the flow parameter is identified, we may be able to predict the responses of plankton to such hydrodynamic signals found in the ocean and possibly relate the plankton distribution to the velocity structure.

Strategically, the escape response of the prey to the hydrodynamic cue should minimize the risk of capture. In Figure 4, many of the distant escapes occurred in areas where the velocity contours are curved which corresponds to areas of high shear while some escapes occurred in the central region close to the mouth where acceleration is high. Since the threshold acceleration to elicit an escape appears high, this hydrodynamic cue may not be a good signal to rely on if the prey would like to stay outside of the capture range of the copepod. For the predator, by creating a flow field which minimizes shear in the region in front of the mouth parts, this copepod enhances prey capture in the area closest to its mouth.

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