CHARACTERISTICS OF THE HIGH FREQUENCY ESCAPE REACTIONS OF *OITHONA SP.*

DAVID M. FIELDS*

*Georgia Institute of Technology, School of Biology, 310 Ferst Dr.,
Atlanta, GA 30332*

The cyclopoid copepod *Oithona* was found to exhibit multiple escape reactions when entrained within quantified flow fields. The distance of the escape from the flow-producing predator mimic (a siphon) decreased with a concurrent decrease in escape distance and speed. Although individuals became behaviorally more sensitive to fluid motion with each successive escape reaction, the lower thresholds were not manifested as more distant escape reactions. Overall, the escape distance and speed decreased significantly with decreased signal strength. The decrease may result from the high cost of the escape reaction, which was calculated to account for 36% of the normal metabolic rate and 500 times the cost of normal swimming.

Keywords: Copepod; *Oithona*; Escape; Water movement; Behavior; Swimming

INTRODUCTION

Copepods have various morphological and behavioral defenses against predators such as gelatinous zooplankton, fish and carnivorous copepods. Their success at implementing defense mechanisms determines their susceptibility to predation, which in turn creates a pattern of selective feeding for specific predators. Understanding these defense mechanisms offer insights into temporal patterns observed in zooplankton communities.

An important behavioral defense mechanism against predation is the rapid escape response. The avoidance response of copepods to stationary objects (Haury *et al.*, 1980), and the escape reaction of copepods to siphon

*Tel.: (404) 894-8430, e-mail: david.fields@biology.gatech.edu

flows (Singarajah, 1969), fish predation (Drenner *et al.*, 1978; Kimmerer and McKinnon, 1989; Svensson, 1992), predatory euphausids (Stuart and Huggett, 1992), predatory cladocerans (Browman *et al.*, 1989), and to the feeding currents of predatory copepods (Fields and Yen, 1993; Fields and Yen, 1996) suggests that it is a prevalent mechanism by which copepods avoid adversities. However, when smaller copepods are being preyed upon by larger predatory copepods an escape reaction does not always free the animal from the risk of predation (Yen and Fields, 1992; Doall, 1995; Fields and Yen, 1997b) and the prey are forced to exhibit multiple escape reactions. The implications of repetitive escape reactions on the effectiveness of the escape are unknown. However, based on force calculations (Alcaraz and Strickler, 1988) the energetic costs of an escape reaction may diminish the effectiveness of repetitive escapes. The present study examines the multiple escape reactions of the copepod *Oithona sp.* in response to a siphon flow. The objectives of this study were to determine if the escape characteristics and its behavioral threshold vary with multiple escapes from an artificial feeding current.

METHODS

Animal Collection

Copepods were collected in a submersed 125 µm net receiving water from the continuously flowing out fall pipe drawing 25°C water from a depth of 20 meters below the surface. The pipe is located at The Natural Energy Laboratory of Hawaii Association (NELHA) on Ke'hole Point Hawaii, HI (Fields and Yen, 1993). Collections took place from 14:00 to 8:00 on 11/(22 – 23)/93. Approximately 200 animals were rapidly sorted and maintained in the 4.5 liter experimental vessel at 24°C overnight. No food was added to the experimental vessel. Experiments were conducted between 7:30 am – 12:30 pm.

Video Recordings

Video observations were made through a 4.5 liter Plexiglas vessel. Filming was done using a Shlieren optical pathway with a single HeNe laser (632.8 nm) as a light source (Strickler, 1985; Yen and Fields, 1992; Fields and Yen, 1993). The 1 mm laser beam was split, expanded to 20 mm and then projected onto 2 perpendicularly mounted video cameras (Pulnix TM – 745) equipped with 100 mm macro-zoom Vivitar lenses. A cube of

approximately 1.6 ml of fluid in the experiment tank was filmed for analysis using a magnification of 10X. Images were recorded on two Panasonic AG-1960 video recorders synchronized with a Comprehensive Video Supply Corporation time code generator. To increase temporal resolution, individual video frames (33 ms) were split and analyzed field by field (16.7 ms). Video analysis was accomplished by digitizing video images on a Gateway 2000® PC equipped with a frame grabbing card and Bioscan Image Analysis® software.

Siphon Tank Configuration

The tank size used was 15 cm × 15 cm × 25 cm (L × W × H) with a working volume of ∼ 4.5 liters. A 0.8 mm outer diameter siphon was mounted in the center of the tank at a height of 5.5 cm above the bottom. A head height of 17.7 cm was maintained by introducing 0.45 μm filtered seawater at the top of the tank through a 6.7 cm vessel at the water's surface

Siphon Flow Analysis

Fluid motion at different points within the siphon flow was determined by tracking neutrally buoyant polystyrene spheres (21 μm) simultaneously from both video cameras. By combining data points that share a similar value (+/− 100 μm) in the Y direction, an essentially planer view of the particle trajectories could be analyzed (Fields and Yen, 1993). Velocity ($\delta S/\delta t$) was calculated as the change in distance (S) over time. The length of time used varied from 2 and 10 fields (33 and 167 ms) depending on the location of the particle in the flow field. The greater the change in distance the smaller the time increment used. At the mouth of the siphon, the flow velocities became too rapid for the temporal resolution of the video cameras and could not be determined by tracking particles. To calculate the flow velocity at the origin of the siphon, the water exiting the siphon was measured by determining the length of time required to fill 100, 250 and 500 ml volumetric flasks at different periods throughout the experiment. Since at the entrance of the siphon the velocity is nearly uniform across the diameter (Vogel, 1981), the total flow ($Q : ml\ s^{-1}$) was used to find the average entry flow velocity (V^*) as:

$$V^* = \frac{Q}{\pi a^2} \tag{1}$$

where 'a' is the radius of the siphon (Vogel, 1981).

Shear was calculated as $\delta U/\delta z + \delta W/\delta x$. Velocities in the X (δU) and Z (δW) directions were taken from contoured velocity data in the horizontal and vertical direction, respectively, using a 0.02 mm separation as δz and δx. The shear data was contoured with grid size of 0.5 mm. Both the measured and calculated points were used in the contouring. Velocity and shear contours were generated using SURFER® contouring software distributed by Golden Software Inc.

Animal Behavior

The mechanics involved in an escape reaction have been previously described for the freshwater copepod *Cyclops sp.* (Strickler, 1975). The escape reaction can involve a single jump in which the antennae are drawn to the sides of the body followed by the motion of the four swimming legs or a series of jumps in which there is one beat of the first antenna followed by multiple cycles of motion in the swimming legs. A single jump and recovery stroke last approximately 20 ms (Strickler, 1975). In this study, the start and end of the escape reactions were characterized as the point at which the first antennae began retracting to the sides of the body and ended when they returned to their pre-escape position. The speed of the animal during the escape reaction was measured as the distance traveled in 33 ms from the time the escape reaction was initiated. Therefore, both single and multiple cycles of the swimming legs were considered a single escape response if the antenna did not return to their original position. The escape distance was calculated as the cumulative distance traveled over the entire escape sequence. The distance was calculated at 16 ms intervals to capture the increased length of a tortuous path. Escape locations were superimposed over contours of fluid shear to determine the stimulus strength at each escape location.

RESULTS

Siphon Flow

The flow into the siphon was radially symmetrical allowing its characteristics to be adequately represented in 2 dimensions. The shape of the speed isolines surrounding the siphon is best described as concentric rings of speed anchored at the center of the siphon's mouth (Fig. 2A). Shear values, in contrast, were minimum directly above the center of the siphon center while the maximum values were at angles of $\sim 35°$ measured from a line vertical to the siphon center (Fig. 2B).
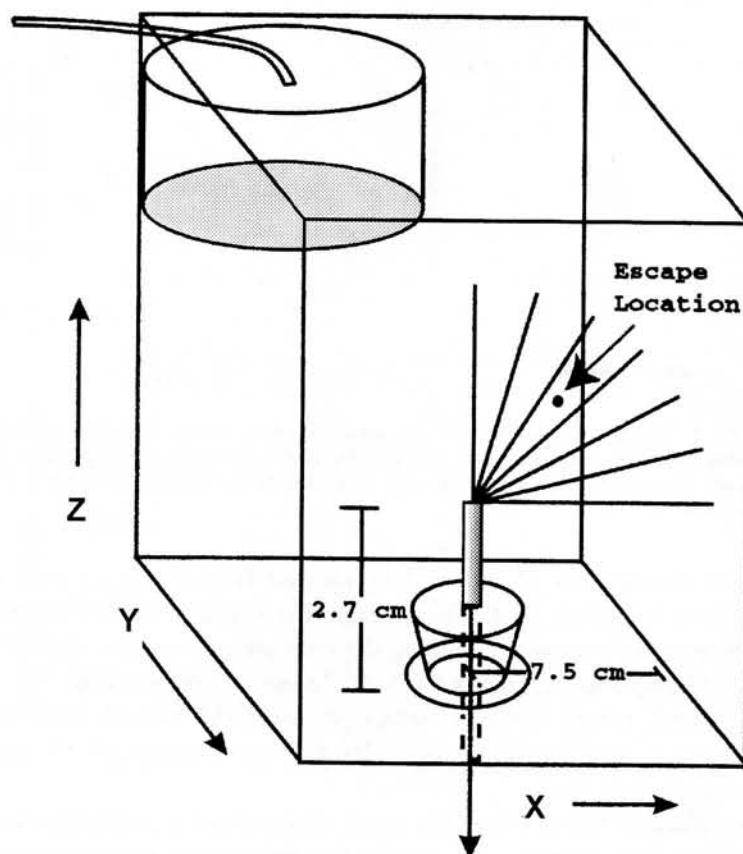
FIGURE 1 Siphon tank. Base of the tank is a square with 140 mm side. Siphon is a 0.6 mm internal diameter (0.8 mm outer diameter) capillary tube with the opening 23 mm from the tanks bottom. Water height is 177 mm above the siphon giving a flow rate of $0.058 \, \text{ml s}^{-1}$.

Animal Behavior

Of the 150 individuals that exhibited successful escape reactions, 22 animals (14%) showed multiple escapes. However, when animals initiated the escape below the top of the siphon the specific location of the animal could not be identified. As a result, for only eight of these animals could the 3-dimensional coordinates be discerned for further analyses.

The multiple escape responses were commonly a series of single jumps followed by a final rapid (Fig. 3A) and more distant (Fig. 3B) escape reaction which often placed the animal in a region near the edge of the filming view. The mean number of escapes for individuals which exhibited
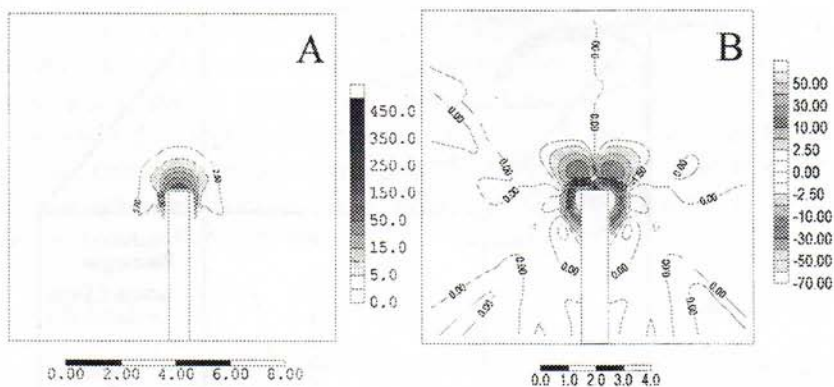
FIGURE 2   Isolines of flow speed (A) and shear (B) into a 0.8 mm O.D siphon. Isolines are calculated from the displacement of neutrally buoyant 21 μm polystyrene particles. Isolines values are given in the corresponding gray scale. Values are reported in $mm\,s^{-1}$ and s^{-1} respectively.

multiple escapes was 5.5 ($+/-$ 3.8), ranging from a maximum of 16 escapes to a minimum of 4. The average distance and speed traveled during the escapes response, excluding the final escape reaction, was 1677-μm ($+/-863\,\mu m$) and 32.9 mm/s ($+/-10.7\,mm\,s^{-1}$), respectively. The mean of the final escape distance, which released the animal from further entrainment, was 3916 μm ($+/-2204\,\mu m$) at a speed of $53.7\,mm\,s^{-1}$ ($+/-22.8\,mm\,s^{-1}$).

The distance traveled and the speed of the escapes, excluding the final escape reaction, showed a strong negative relationship with the number of escapes (Tab. I). For each escape attempt the distance traveled was 79.3 μm less then the previous jump and the speed of the escape was $1.3\,mm\,s^{-1}$ slower with each successive attempt. The speed and distance traveled during the final escape reaction was negatively correlated with the previous number of escape reactions although the regression was not significant (Tab. II).

The distance from the source at which the escape reaction was initiated showed a significant negative relationship with the number of escapes (Fig. 3C). The average distance from the siphon center for all the escapes, excluding the final escape reaction, was 1330 μm. Each successive jump was on average initiated 21 μm closer to the source than the previous leap.

The threshold shear value needed to elicit the escape reaction decreased significantly with each successive escape reaction (Fig. 4). The relationship between the escape characteristics and the stimulus strength suggests a slight
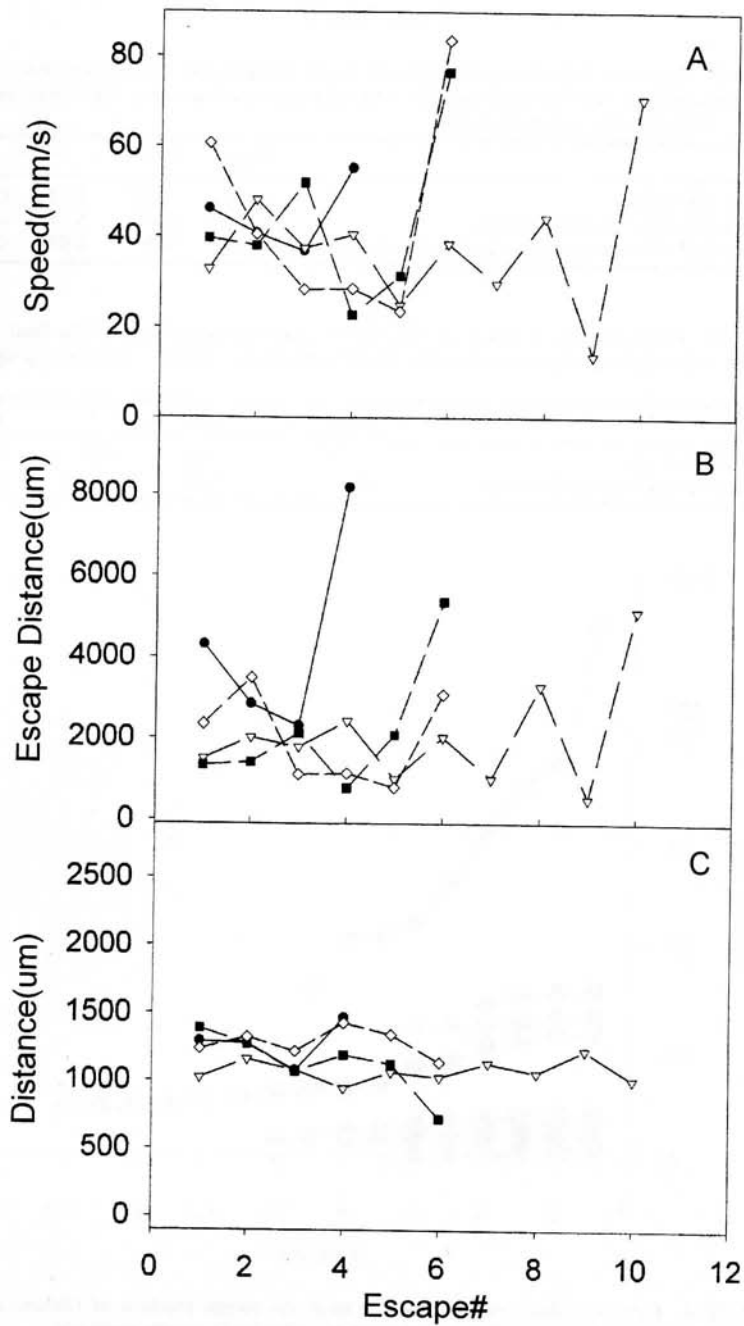
FIGURE 3 Escape speed (A), travel distance (B) and distance from the pipette when the escape was initiated (C) of four copepods with respect to each successive jump. Different symbols represent different individuals. For clarity, only select animals analyzed in this study are shown.

TABLE I Parameters for a linear fit of different escape characteristics to the sequence in which the escape occurred. The final rapid escape is omitted from the calculations. Speed is reported in mm s^{-1}. Distances are reported in μm

	Slope	Y(0)	r^2	P
Speed of the escape	−1.3	39.5	0.18	< 0.001
Distance traveled during the escape	−79.3	2069	0.11	< 0.01
Distance from the source when the escape is initiated	−21.8	1443	0.07	< 0.05

TABLE II Parameters for a linear fit of different escape characteristics of the final escape reaction to the number of previous escapes. Speed is reported in mm s^{-1}. Distances is reported in μm

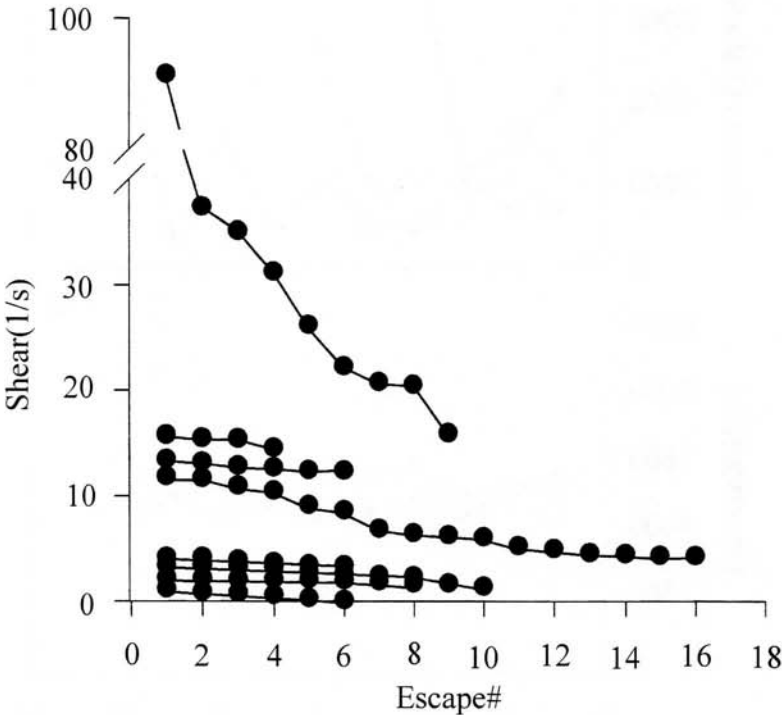|	Slope	Y(0)	r^2	P
Speed of the escape	−3.3	83	0.20	ns
Distance traveled during the escape	−371.1	7114	0.11	ns

FIGURE 4 Threshold shear value needed to elicit the escape reaction of *Oithona sp.* as a function of escape number. Each line represents an individual's escape sequence.

yet significant dose response. The escape speeds and distances traveled by the animals showed a significant positive relationship to the shear value at the point of escape (Tab. III).

TABLE III   Parameters for a linear fit of different escape characteristics to the shear value at which the escape occurred. The final rapid escape was omitted from the calculations. Speed is reported in mm s^{-1}. Distances is reported in μm

	Slope	Y(0)	r^2	P
Speed of the escape	0.38	32	0.11	< 0.01
Distance traveled during the escape	27	1715	0.07	< 0.05

One explanation for the decay in escape magnitude with successive jumps may be the result of the decreased physiological ability of the animal to perform repetitive energetically expensive behaviors. To examine this, the escape data was used to calculate the energy consumed during an escape and then compared that value to the energy consumed by normal metabolism for these animals. The force (F) needed for an escape reaction can be calculated as:

$$F = M_v * a_1 + F_d \qquad (2)$$

where M_v is the virtual mass, a_1 is the acceleration rate and F_d is the force due to drag. Virtual mass is defined as the mass of the object and the apparent added mass (Vogel, 1981). For a cylinder normal to the flow the apparent added mass and the mass of the object are approximately equal. The mass (M) can be determined (in mg) as a function of length for *Cyclops* (Klekowski and Shushkina, 1966) as:

$$M = 0.055 * l^{2.73} \qquad (3)$$

where l is the length of the animal in mm. Using the average animal length of 0.697 mm found in this study, the mass of the animals are 0.0206 mg. The maximum acceleration rate found in this study was 896 cm s^{-2} compared with 1200 cm s^{-2} found by Strickler (1975) who used high speed filming with resolution of 4 ms. Drag (F_d) can be estimated as:

$$F_d = (1/2) * C_d * r * A * U^2 \qquad (4)$$

with C_d being the coefficient of drag, r as the density of sea water, A as the frontal area and U representing the velocity of the animal. The coefficient of drag (C_d) can be expressed as a function of the Reynolds number (Vogel, 1981). The Reynolds number was calculated to be ~ 50 for a 0.7 mm animal traveling at 35 mm s^{-1}. Vlymen (1970) found that the C_d was related to the Reynolds number as:

$$C_d(\text{Re}) = \frac{85.2}{\text{Re}^{0.80}} \qquad (5)$$

which results in a C_d of 3.7. The projected area A was empirically solved for *Labidocera trispinosa* as:

$$A = 0.034003 * l^{1.4208} \tag{6}$$

where A is reported in cm^2 and L given in cm. The drag force for an animal with a 0.0698 cm metasome length and a C_d of 3.7 will be $1.8 * 10^{-7} N$. Therefore, the initiation of an escape response requires $3.7 * 10^{-7} N$ of thrust and $1.8 * 10^{-7} N$ to over come drag. The distance traveled during this maximum escape response was 1.4 mm making the total work required to initiate the escape equal to $-5.5 * 10^{-10} J$. The time frame of the initial portion of the escape is 0.0167 ms requiring a power output of $2.8 * 10^{-5} cal\, h^{-1}$. This cost of escape can be then compared to the normal metabolic consumption rates. Normal metabolic consumption rates can be calculated as:

$$QO_2 = 1.22 * M^{0.84} \tag{7}$$

where M is the Mass calculated from length in Eq. (3) (converted to mg for this calculation) and QO_2 is the O_2 consumption rate in ml $O_2 * 10^{-3} h^{-1}$ ind^{-1} (Shushkina *et al.*, 1968). Assuming the caloric equivalent of oxygen is $4.86 * 10^{-5} cal\, ml\, O_2^{-1}$ (Alcaraz and Strickler, 1988) *Oithona*, with an average length of 698 mm, will have a total energy consumption rate of $7.5 * 10^{-5} cal\, h^{-1}$. Comparing the cost of the escape with cost of normal metabolism suggests that the escape reaction can account for 36% of the normal metabolic rate and be over 500 times the cost of normal swimming based on the 0.069% reported for *Cyclops* by Alcaraz and Strickler (1988).

DISCUSSION

The effectiveness of an escape reaction varies as a function of (1) the distance from the predator at which the escape is elicited; (2) the distance and speed of the prey's escape reaction, and (3) the direction of the escape reaction (Fields and Yen, 1997a). In this study the repetitive escape reactions of *Oithona* were examined to determine the change in the escape characteristics as a result of frequent repetitive escape reactions.

Reaction Threshold

The shear value needed to initiate the escape decreased with each successive escape reaction (Fig. 4). This suggests that once alerted to a potential

predator, the prey become behaviorally more sensitive to a fluid mechanical disturbance and elicit an escape reaction more readily. By maintaining a relatively high threshold prior to detecting a potential predator, the prey may minimize the metabolic expense of unnecessary escape reactions (Alcaraz and Strickler, 1988) and minimize detection by both mechanoreceptive and visual predators (Zaret, 1980). However, this result is in stark contrast to the decreased sensitivity reported for *Centropages hamatus* in response to an oscillating stimulus (Hwang, 1991). *C. hamatus* was found to decrease the frequency of the escape reaction when confronted with a continuous high level of turbulence. This apparent discrepancy can be explained in two ways. Hwang (1991) measured threshold values in terms of fluid velocity not fluid shear. Although individual mechanoreceptors in effect are velocity sensors, it is only when the sensor moves relative to the copepods body that a behavioral response is elicited. Conditions necessary for relative motion of the sensor arises only when there is a velocity gradient (Yen and Fields, 1992; Fields and Yen, 1996). As a result, the fluid speed associated with the escape location may have increased, as shown by Hwang, while the shear threshold decreased in value. A second hypothesis is that copepods can distinguish flow patterns created by different sources. Organized laminar shear fields such as that created by suction feeders and the siphon flow used in this study may present a stimulus distinguishable from the "less" repeatable fluid disturbances created by an oscillating grid.

Although the escape threshold decreased, this was not manifested as escape reactions initiated at greater distances from the source (Fig. 3C). In fact, the contrary was true. Each successive escape occurred 21 µm closer to the source than the previous escape. This suggests that the escape reaction prior to its final rapid escape would be 115 µm closer than the first jump based on the 5.5 multiple escape average. Using the observed maximum number of consecutive jumps (16), the escape location could occur up to 336 µm (0.48 body length) closer to the source. If the siphon were a predatory copepod, the decreased distance would have led to an increase in capture success (Doall, 1995) making each repetitive escape less effective for predator avoidance than the previous escape. Since the shear value increases along a given trajectory, these results suggest that the escape reaction transported the animal to a trajectory with lower shear values at a comparable distance. These results are consistent with the findings of Fields and Yen (1997b) on the orientation of copepods in sheared flows. The fluid shear in a suction flow orients bottom heavy copepods towards the region with the most rapid flow. This region of most rapid flow coincides with the

region of lowest shear values at a given distance. This suggests that the copepods are escaping towards the center of the suction flow were they are experiencing less shear and hence initiating escape reactions closer to the flow source.

Escape Distance and Speed

Each successive escape reaction propelled the escaping animal less distance than the previous escape and did so at a significantly slower rate. Depending on the number of sequential escape reactions, the effectiveness of the escape could be greatly diminished. For example, if the animals perform the average number of escape reactions (5.5) prior to their rapid final escape, the next to the last escape would propel the animal 436 µm less distance (0.63 body length) and 7.2 mm s^{-1} slower than the first escape response. The decreased strength of the escape reaction along with the decreasing distance from the source at which the animals initiate their escape can increased the vulnerability of the prey to predation.

The decline in the escape performance may have several explanations. First, the escape reactions may just be an artifact of our measurement techniques. Escape reactions initiated closer to the source are subject to higher flow speeds. The net effect is that the measured escape speeds are underestimated. To estimate the true magnitude of the escape, the escape speed was compared with the flow speed at the escape location. At a distance of 1.3 mm (the average location of the escape) a decrease in escape location gives rise to an increase in flow speed at a rate of ~ 0.5 mm s^{-1} per 100 µm. Thus the average decrease in escape distance of 79 µm with each successive escape can explain 0.4 mm s^{-1} decrease in the escape speed or 31% of the measured 1.3 mm s^{-1} change. This suggests that an increase in flow speed offers a significant but not sufficient explanation for the decrease in escape performance. As a result, the actual strength of the escape, in terms of force output for the prey, decreases with each escape.

A second reason for the slow decay in escape magnitude with successive jumps may result from the animals becoming fatigued. The data suggest that the metabolic cost of an escape reaction can be expensive. The escape reaction accounts for 36% of the normal metabolic rate and over 500 times the cost of normal swimming based on the 0.069% reported for *Cyclops* by Alcaraz and Strickler (1988). This finding compares well with Strickler's (1977) findings that the energy expended in an escape reaction of a cyclopoid copepod can be up to 400 times that of normal swimming. With escape reactions being such an expensive endeavor, recovery from such an event

may be highly time dependent. This high cost may determine the maximum rate of the escape reactions and the number of successive escapes the animal is able to perform. Yet it is clear that fatigue can not be the only explanation for the decrease in the escape reaction since most animals were able to perform a final powerful escape.

A third explanation as to why the strength of the escape reactions may decrease is that the signal strength may decrease. When the prey escape they jump towards the center of the flow field where there is decreased signal strength. Since there was a significant dose response in the escape strength with respect to strength of the signal that elicits the escape reaction (Tab. III), the decreased power of escape may be a reflection of the decreased signal strength.

When confronted with a predator that creates a constant flow field, such as that created by many predatory copepods (Fields and Yen, 1993), a decrease in escape performance can greatly decrease the chance of escape. In addition to being more easily captured, each successive escape sends a pulse of water towards the predator with a force of $5.5 * 10^{-7}$ N. The water bolus contains both chemical signals (urea or other metabolites) and physical information that reflects the prey's size and distance (Legier-Visser et al., 1986). Multiple escape reactions in this situation offers the predator multiple samplings of the preys location which further diminishes the preys chances for a successful escape. However, minimizing the strength of the escape reactions may not always increase the risk of predation. When confronted with a predator that creates a punctuated flow field, such as that created by a suction feeding fish, the copepod need only escape a small distance to avoid the limited volume of fluid that the predator can take. Excessive escapes by the prey incur both a metabolic cost and an increased probability of being detected by the visual – mechanoreceptive predator. Thus there may be a trade off in using the different strategies. This may help to explain the varied response shown by this population of copepods.

References

Alcaraz, M. and Strickler, J. R. (1988) Locomotion in copepods: patterns of movement and energetics of *Cyclops*. *Hydrobiologia*, **167/168**, 409–414.

Browman, H. I., Kruse, S. and O'Brien, W. J. (1989) Foraging behavior of the predaceous cladoceran, *Leptodora kindti*, and escape responses of their prey. *J. Plankt. Res.*, **11**, 1075–1088.

Doall, M. H. (1995) The searching behavior, attack volume, and capture efficiency of *Euchaeta rimana*, a predatory calanoid copepod. *M.S. Thesis*, SUNY Stony Brook.

Drenner, R. W., Strickler, J. R. and O'Brien, W. J. (1978) Capture probability: The role of zooplankter escape in the selective feeding of planktivorous fish. *J. Fish. Res. Bd. Canada*, **35**, 1370–1373.

Fields, D. M. and Yen, J. (1993) Outer limits and inner structure: The 3-dimensional flow field of *Pleuromamma xiphias* (Calanoida: Metridinidae). *Bull. Mar. Sci.*, **53**, 84–95.

Fields, D. M. and Yen, J. (1996) The escape behavior of *Pleuromamma xiphias* from a quantifiable fluid mechanical disturbance. In: *Zooplankton: Sensory Ecology and Physiology*. Lenz, P. H., Hartline, D. K., Purcell, J. E. and Macmillan, D. L. (Eds.), pp. 323–340. Gordon and Breach Publ., Amsterdam.

Fields, D. M. and Yen, J. (1997a) The escape behavior of marine copepods in response to a quantifiable fluid mechanical disturbance. *J. Plankton Res.*, **19**, 1289–1304.

Fields, D. M. and Yen, J. (1997b) Implication of copepod feeding currents on the spatial orientation of their prey. *J. Plankton Res.*, **19**, 79–85.

Haury, L. R., Kenyon, D. E. and Brooks, J. R. (1980) Experimental evaluation of the avoidance reaction of *Calanus finmarchicus*. *J. Plankt. Res.*, **2**, 187–202.

Hwang, J.-S. (1991) Behavioral responses and their role in prey/predator interactions of a calanoid copepod, *Centropages hamatus*, under variable hydrodynamic conditions. *Ph.D. Thesis*, Boston University.

Kimmerer, W. J. and McKinnon, A. D. (1989) Zooplankton in a marine bay. III. Evidence for influence of vertebrate predation on distribution of two common copepods. *Mar. Ecol. Prog. Ser.*, **53**, 21–35.

Klekowski, R. Z. and Shushkina, E. A. (1966) Ernärhung, Amtung, Wachstum, und Energie-Umformung in Macrocyclops albidus jurine. *Verh. int. Ver. Limnol.*, **16**, 399–418.

Legier-Visser, M. F., Mitchell, J. G., Okubo, A. and Furhman, J. A. (1986) Mechanoreception in calanoid copepods: A mechanism for prey detection. *Mar. Biol.*, **90**, 529–535.

Shushkina, E. A., Anisimov, S. I. and Klekowski, R. Z. (1968) Calculation of production efficiency in plankton copepods. *Pol. Arch. Hydrobiol.*, **15**, 251–261.

Singarajah, K. V. (1969) Escape reaction of zooplankton: the avoidance of a pursuing siphon tube. *J. Exp. Mar. Biol. Ecol.*, **3**, 171–178.

Strickler, J. R. (1975) Swimming of planktonic *Cyclops* species (Copepoda, Crustacea): Pattern, movements and their control. In: *Swimming and flying in nature*, Wu, T. Y. T., Brokaw, C. J. and Brennen, C. (Eds.), Plenum Press, Princeton.

Strickler, J. R. (1977) Observations of swimming performances of planktonic copepods. *Limnol. Oceanogr.*, **22**, 165–169.

Strickler, J. R. (1985) Feeding currents in calanoid copepods: Two new hypotheses. In: *Physiological Adaptations of Marine Animals*, Laverack, M. S. (Ed.), The Company of Biologists Limited, Cambridge.

Stuart, V. and Huggett, J. A. (1992) Prey selection by *Euphausia lucens* (Hansen) and feeding behavior in response to mixed algal and animal diet. *J. Exp. Mar. Biol. Ecol.*, **164**, 117–133.

Svensson, J. E. (1992) The influence of visability and escape ability on sex-specific susceptibility to fish predation in *Eudiaptomu gracilis* (Copepoda, Crustacea). *Hydrobiologia.*, **234**, 143–150.

Vlymen, W. J. (1970) Energy expenditure by swimming copepods. *Limnol. Oceanogr.*, **15**, 348–356.

Vogel, S. (Ed.) (1981) *Life in Moving Fluids: the Physical Biology of Flow*. 1st edn., Vol. 1. Willard Grant Press, Boston.

Yen, J. and Fields, D. M. (1992) Escape responses of *Acartia hudsonica* (Copepoda) nauplii from the flow field of *Temora longicornis* (Copepoda). *Arch. Hydrobiol. Beih. Ergebn. Limnol.*, **36**, 123–134.

Zaret, T. M. (1980) The effect of prey motion on planktivore choice. pp. 594–603. In: *Evolution and Ecology of Zooplankton Communities*. Kerfoot, W. C. University Press of New England, Hanover.