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The escape behavior of marine copepods in response to a quantifiable fluid mechanical disturbance

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Abstract. The threshold shear values needed to elicit the escape reaction to a quantifiable fluid mechanical disturbance were compared between five free-swimming oceanic copepod species. The results indicate a significant difference in the threshold for different species of copepods and between different age groups within a single species. In general, animals captured from more energetic regimes required a higher threshold than those captured from more pacific locations. *Labidocera madurae* required the highest shear values with 51.5 s^{-1} for 50% of the animals tested to elicit an escape reaction (S_{50}). *Acartia tonsa* and *Euchaeta rimana*, in contrast, were behaviorally the most sensitive requiring an S_{50} of only 1.5 and 4.1 s^{-1}, respectively, to initiate an escape reaction. *Pleuromamma xiphias* and *Oithona* required intermediate shear values with an S_{50} of 7.2 and 8.1 s^{-1}. When compared to literature values, the threshold needed to elicit an escape reaction was consistently higher than average environmental shear values. Threshold shear values also varied significantly with developmental stage. Naupliar stages of *A.tonsa* required greater than six times the S_{50} value required by adults of the same species. This suggests that the higher vulnerability to predation of naupliar stages of copepods may not only reflect inferior escape strength, but may also result from the higher threshold needed to elicit an escape reaction. This study supports the hypothesis that selective feeding patterns exhibited by predators of copepods may be the result of the differential behavioral sensitivities of different species and developmental stages of copepods.

Introduction

Predation acts as a major force controlling the dynamics and structure of planktonic communities. For a predator, an unsuccessful predation event results only in its continued hunger. For the prey, an ineffectual deterrent to predation results in its own demise and removal from the reproducing population. With such a strong selective pressure, the ability of a prey to avoid predation is crucial and the selection for offenders swift.

In an effort to understand the structuring role of predation, trophic ecologists have long sought to predict the risk of particular prey to specific predators. Selective feeding is recognized as an important mechanism by which planktonic communities are structured by predation. Therefore, understanding the mechanisms of selective feeding is important for interpreting the dynamics of predator–prey populations. For copepods, the escape behavior is probably the most immediate and effective anti-predatory strategy. Differences in the escape abilities of different species of copepods may be manifested as greater electivity for particular prey. The successful escape has two fundamental components, both of which are necessary to minimize predation. First, the prey must be able to detect their predators remotely. Second, the prey must be able to elicit a rapid and directional escape reaction. Several studies have documented the rapid escape abilities of

copepods (Strickler, 1975); however, little work has been done which addresses the stimulus needed to elicit the escape reaction in different copepods. Yet, differences in the timing of the escape between co-existing species may make one species of prey more susceptible to predation than another.

Mechanoreception is considered an important mechanism for the remote detection and discrimination of predators (Strickler and Bal, 1973; Landry, 1980; Legier-Visser *et al.*, 1986; Bleckmann *et al.*, 1991; Yen *et al.*, 1992). The presence of mechanoreceptive setae on the first antennae of copepods is well known (Strickler and Bal, 1973; Kurbjeweit and Buchholz, 1991). Numerous species have shown the ability to detect nanometers of fluid displacement (Yen *et al.*, 1992). With such strong mechanoreceptive capabilities, it is curious why copepods are not constantly exhibiting an escape reaction. This discrepancy underscores the paucity of data addressing the relationship between the thresholds needed to elicit neurophysiological activity versus that needed to elicit behavioral responses. Recently, Fields and Yen (1996) examined the fluid mechanical signal which elicited the escape reaction in *Pleuromamma xiphias* using a siphon flow as a mechanism to produce a quantifiable fluid mechanical signal. Fluid shear was found to be the least variable characteristic eliciting the escape reaction and best explained the pattern of escape surrounding the siphon. Implicit in the hypothesis that selective feeding is in part driven by the differential behavior of co-existing prey is that the behavioral sensitivity of copepods is species specific. However, little is known about how the shear value needed to elicit the escape reaction in *P.xiphias* relates to the critical shear value of other copepod species.

The work described herein is a continuation of the previous study examining the escape reaction of *P.xiphias* (Fields and Yen, 1996). In the present study, the escape thresholds of four additional oceanic species of copepods were determined. *Euchaeta rimana* and *Oithona* are pelagic open-water copepods. *Acartia tonsa* is a pelagic nearshore copepod (Paffenhöfer and Stearns, 1988) found in waters with a depth of 20 m. *Labidocera madurae* is found primarily at the surface in shallow, highly energetic waters. The animals were chosen as representatives of three distinct habitats: a strong vertical migrator with a 700 m daytime maximum and 50 m night-time maximum (*P.xiphias*), offshore upper water column animals (*E.rimana* and *Oithona*) and animals from a highly energetic environment (*L.madurae* and *A.tonsa*). The hypothesis tested in this study is that all species of copepods require the same threshold shear value to elicit an escape reaction.

Method

Animal collection

Euchaeta rimana and *Oithona* were selected from pump samples collected at a depth of 15 m and ~100 m offshore from the Natural Energy Laboratory of Hawaii Association (see Fields and Yen, 1996). *Pleuromamma xiphias* was collected at the same facility from a depth of 585 m. *Labidocera madurae* were collected at night from Keauhou Bay (HI) on the Island of Hawaii using sampling jars and an underwater flash light. *Acartia tonsa* were from laboratory cultures, initially collected from Long Island Sound, grown in natural light conditions with

Thalassiosira weissflogii as their only food source. Approximately 300 animals of each type were sorted and brought to 22°C over a 24 h period prior to filming for each experiment.

Video recordings

Video observations of copepods were made in two ways depending on the size of the animals being filmed. For the larger animals (*E.rimana, L.madurae* and *P.xiphias*), video observations of copepods were made through a 22 l Plexiglas vessel (Fields and Yen, 1996). A cube of ~200 ml of fluid surrounding the siphon was filmed for analysis using a magnification of 3.5–5×. The video cameras were two perpendicularly mounted Pulnix TM-745 equipped with 28–70 macro-zoom Vivitar lenses. The cameras were fixed to a Newport motion isolated table. The tank was illuminated from above with two fiberoptic Shotts lamps covered with a Kodak Wratten Gelatin Filter (#24) to shift the light spectrum into the red. The images were recorded on two Panasonic AG-1960 video recorders which were synchronized with a Comprehensive Video Supply Corporation time code generator. Video analysis was accomplished by digitizing video images on a Gateway 2000 PC equipped with a frame-grabbing card and Optimus video analysis software created by Bioscan.

For the smaller animals (*Oithona* and *A.tonsa*), the filming was carried out using a modified Schlierin optical set-up described in detail elsewhere (Strickler, 1985; Fields and Yen, 1993). The tank was illuminated with a HeNe laser (Newport) and was filmed using the camera and recorders described above. Using the Schlierin set-up, a cube containing 2.0 ml of water was filmed within a 4.5 l vessel with a realized magnification of ~20×.

Siphon configuration

Pleuromamma xiphias, E.rimana, L.madurae. The siphon configuration is as described in Fields and Yen (1996) for the escape response of *P.xiphias*. A brief description is included here for the sake of completeness. The siphons were made from stock Cornix Pyrex glass tubes mounted in the center of the 22 l filming vessel at a height of 73–80 mm from the tank's bottom. A siphon with a 7.0 mm outer diameter (OD), a 5.0 mm OD or a 3.0 mm OD was used to create the fluid disturbance. A constant head height, different for each siphon, was maintained to create a steady flow rate into the siphon. The constant head height was maintained by simultaneously replacing the exiting water with 0.45 μm filtered seawater (FSW). To diminish the disturbance to the siphon flow, incoming water was introduced into a 10.5 cm diameter vessel which drained through a 35 μm mesh screen located at the water's surface. Fluid motion at different points within the siphon flow was determined by tracking neutrally buoyant *Artemia* eggs (~200 μm in diameter) entrained by the flow simultaneously from both video cameras. Not all the animals were tested against all the siphons. Details of the experimental conditions and siphon–animal combinations are shown in Table I.

Oithona and A.tonsa. Tank configuration, in general, was a scaled down version of that described above. The tank size used was 15 × 15 × 25 cm (L × W × H) with a working volume of ~4.5 l. The siphons used, again mounted in the center of the tank, were either a 3.0 mm OD or a 0.8 mm OD, the height of which was 2.7 cm above the bottom of the tank. A head height of either 8.3 or 17.3 cm was maintained by introducing FSW at the top of the tank through a 6.7 cm vessel at the water's surface. Flow velocities were determined as above using 21 μm polystyrene spheres as flow markers.

Flow analysis

Velocity ($\delta L/\delta t$) and shear ($\delta U/\delta z$) + ($\delta W/\delta x$) were computed as in Fields and Yen (1996), where L is the total particle displacement in all three dimensions, and U and W are velocities in the X and Z directions, respectively. Near the mouth of the siphon, flow velocities were too rapid to characterize accurately using particle trajectories. Flow speeds across the mouth of the siphon were calculated as in Fields and Yen (1996) using an exiting rate (Q) of 1.03 ml s^{-1} for siphon 5 and 0.053 ml s^{-1} for siphon 6. Exiting rates for siphons 1–4 are detailed in Fields and Yen (1996). Velocity and shear contours were generated using SURFER contouring software distributed by Golden Software.

Fluid mechanical signal at the point of escape

Escape locations were plotted with contours of shear to generate histograms of the frequency of escape as a function of the different shear values for the five animal species. Different siphon configurations were used to uncouple the fluid characteristics at the point of escape. *Pleuromamma xiphias* was exposed to four siphon configurations, *E.rimana* was exposed to three, and *L.madurae* and *Oithona* to two different siphons. Both *A.tonsa* adults and nauplii were exposed only to the 0.8 mm OD siphon. Since the shear values at the point of escape were not found to be normally distributed, as found in the previous study of *P.xiphias* (Fields and Yen, 1996), frequency distributions used to compare the critical shear values for the different species were tested using a Mann–Whitney U-test (Sokal and Rohlf, 1981). Before combining the results from different siphon configurations, frequency distributions were tested using a Kruskal–Wallis test for each species exposed to more than two siphons and a Mann–Whitney U-test for two-sample experiments. Once combined, the shear value at which 50% of the escapes occurred (S_{50}) was used as the quantitative measure to compare the escape threshold for the different species tested. The S_{50} was calculated by plotting the cumulative probability of escape as a function of the bin value for the shear.

Results

Siphon characteristics

A detailed description of siphons 1–4 can be found in Fields and Yen (1996). Shear isolines for siphons 5 and 6 are shown in Figure 1. General features of the shear patterns created by the siphon intake are regions of low shear directly

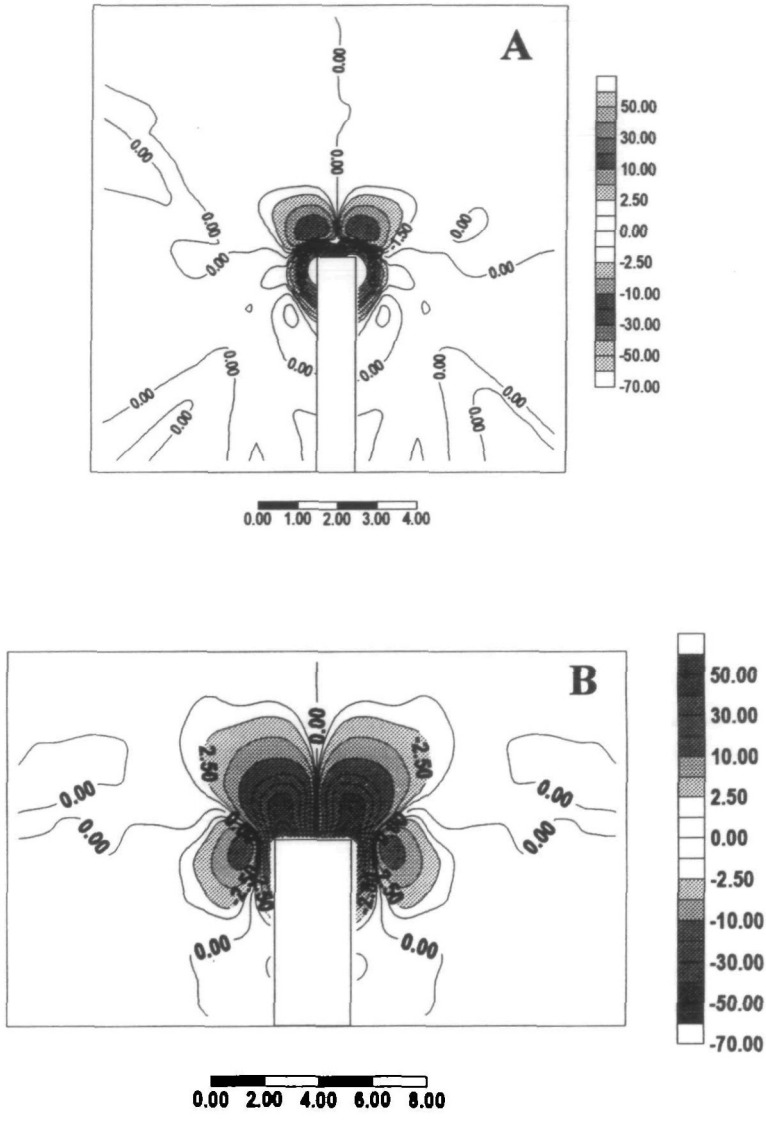

Fig. 1. Isolines of flow shear into a 0.8 mm OD (**A**; siphon 6) siphon and a 3.0 mm OD (**B**; siphon 5) siphon. Isolines are calculated as changes in velocity of neutrally buoyant 21 μm polystyrene particles. Isolines values are given in the corresponding color band. Values are reported in s^{-1}.

above and lateral to the siphon. Regions of maximum shear are created at angles of ~35° measured from a vertical line through the medial axis of the siphon.

Escape frequency and distance as a function of location around the siphon

Before pooling the data for each species tested against multiple siphons, the escape distributions were compared using a Kruskal–Wallis (K–W) test. Table I

Table I. External diameter of siphons and the height of the water above the siphon mouth for each experimental set-up. The number of escape reactions analyzed for each species tested is shown for the different siphons. The Kruskal–Wallis (K–W) probability is given for the difference between the escape distributions from different siphons for each species

Animal	K–W	Siphon (mm)	1	2	3	4	5	6
			7.0	7.0	5.0	3.0	3.0	0.8
		Head height (mm)	127	77	177	177	83	173
E.rimana	0.54		*	81	44	1	*	*
P.xiphias	0.33		70	43	45	14	*	*
L.madurae	0.69		*	65	*	8	*	*
Oithona	0.004		*	*	*	*	93	149
A.tonsa adult			*	*	*	*	*	17
A.tonsa nauplii			*	*	*	*	*	149

*No data collected

shows the number of escapes from each of the siphons and the K–W test results. Of the four species which were tested with multiple siphons, only *Oithona* showed a significant difference in the escape distributions. The significance resulted from few escape reactions which occurred at very high shear values in the 0.8 mm OD siphon. When the escape reactions with the highest thresholds (10 animals) were removed from the distribution profile, the results from the siphons were statistically indistinguishable. For comparison with the other species, the results of the two siphons for *Oithona* were considered to represent a single population.

The distribution of escapes surrounding the siphons is shown in Figure 2. For comparison, the distributions of escapes for larger copepod species (*E.rimana, P.xiphias* and *L.madurae*) are shown for the 7.0 mm OD siphon. For the smaller copepods (*Oithona, A.tonsa* adults and nauplii), the escape locations surrounding the 0.8 mm OD siphon are used. Immediately evident in the larger species is the low number of escapes which occur directly above the siphon. This is the region of minimum shear. Escape distances between the species were significantly different ($P < 0.05$ *P.xiphias* versus *E.rimana*; $P < 0.05$ *P.xiphias* versus *L.madurae*; $P < 0.001$ *E.rimana* and *L.madurae*; Mann–Whitney *U*-test). *Euchaeta rimana* showed the most distant escapes with 13% of the total occurring at a distance >20.0 mm from the siphon center. The average distance from the siphon center at which *E.rimana* initiated its escape reaction was 11.8 mm (± 6.2 mm). *Labidocera madurae* were entrained the closest to the siphon center before eliciting an escape reaction with 84% of the escapes occurring at a distance of <10.0 mm. The mean distance for the initiation of the escape reaction was 8.6 mm (± 5.2 mm). *Pleuromamma xiphias* showed an intermediate escape location of 9.5 mm (± 4.0 mm). Distances were not normally distributed ($P < 0.001$ for all), but rather were skewed to the right ($g_1 = 1.7$ for *P.xiphias*, 1.3 for *E.rimana*, 3.4 for *L.madurae*), suggesting that the escape reactions occurred more frequently at a greater distance from the mean than a delayed escape reaction which would have occurred closer to the mouth.

Of the smaller species examined, *A.tonsa* adults proved to be the most sensitive with 24% of the escapes occurring at a distance >2.0 mm. The average distance of escape was 2.8 mm (± 1.9 mm). *Acartia tonsa* nauplii escaped the closest

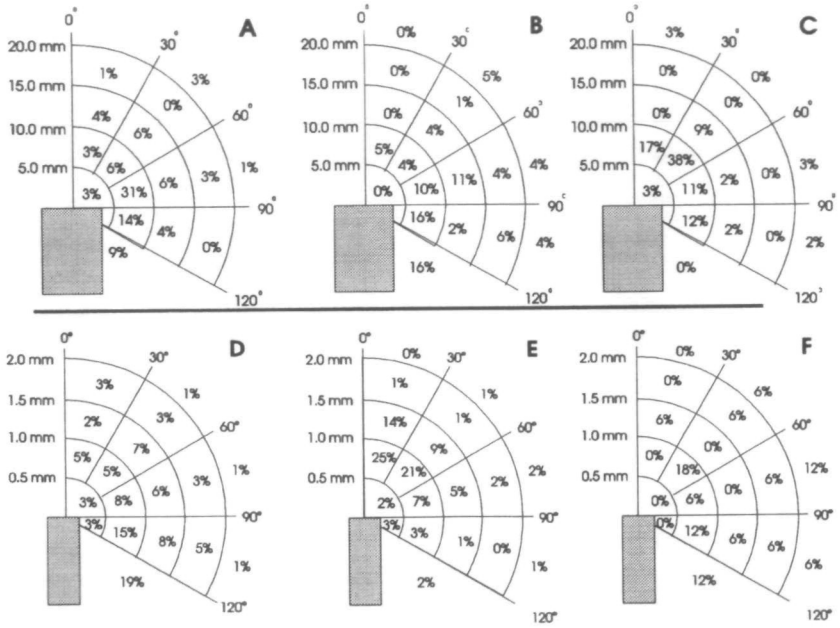

Fig. 2. Frequency distributions of the escape responses of *P.xiphias* (**A**), *E.rimana* (**B**), *L.madurae* (**C**), *Oithona* (**D**), *A.tonsa* nauplii (**E**) and *A.tonsa* adults (**F**) with respect to the geographical regions surrounding each siphon. (A–C) show the escape reactions to siphon 2 (7.0 mm OD), while (D–F) are escape locations from siphon 6 (0.8 mm OD). Regions are demarked by both distance and angle from the siphon center. Each arc represents an equal distance from the siphon center. Angles are in increments of 30° measured clockwise from the vertical line through the siphon center.

to the siphon with an average distance of 1.1 mm (± 0.3 mm), while *Oithona* showed an intermediate value of 1.3 mm (± 0.6 mm). Frequency distributions of the distances were significantly ($P < 0.001$; Mann–Whitney U-test) different from each other. As with the larger species, very few escapes occurred directly above the siphon, although *A.tonsa* nauplii were the least discriminate, showing no clear pattern in the escape distribution.

Escape frequency as a function of shear rates

Frequency distributions for all the animals are shown in Figure 3. Bin values were chosen to give maximum separation at shear values below one. Subsequent values are given in intervals of 5 s^{-1}. *Acartia tonsa* escaped at the lowest shear value with an S_{50} of 1.5 s^{-1}. Less than 6% of the escapes occurred at shear values >7.5 s^{-1}, while over 35% occurred below 0.75 s^{-1}. Of the larger copepods, *E.rimana* escaped at the lowest shear values with 50% of the escapes occurring below a shear value of 4.1 s^{-1} (S_{50}). Less than 14% of the escapes occurred above 50 s^{-1} and <20% occurred at values below 0.75 s^{-1}. *Oithona* and *Pleuromamma* and *A.tonsa* nauplii were found to have a similar distribution in their escape patterns with <10% of the escapes occurring above 60 s^{-1} (35 s^{-1} for *A.tonsa*) and fewer than 15% below 0.75 s^{-1}. An S_{50} of 8.1 s^{-1} was found for *Oithona, P.xiphias* showed

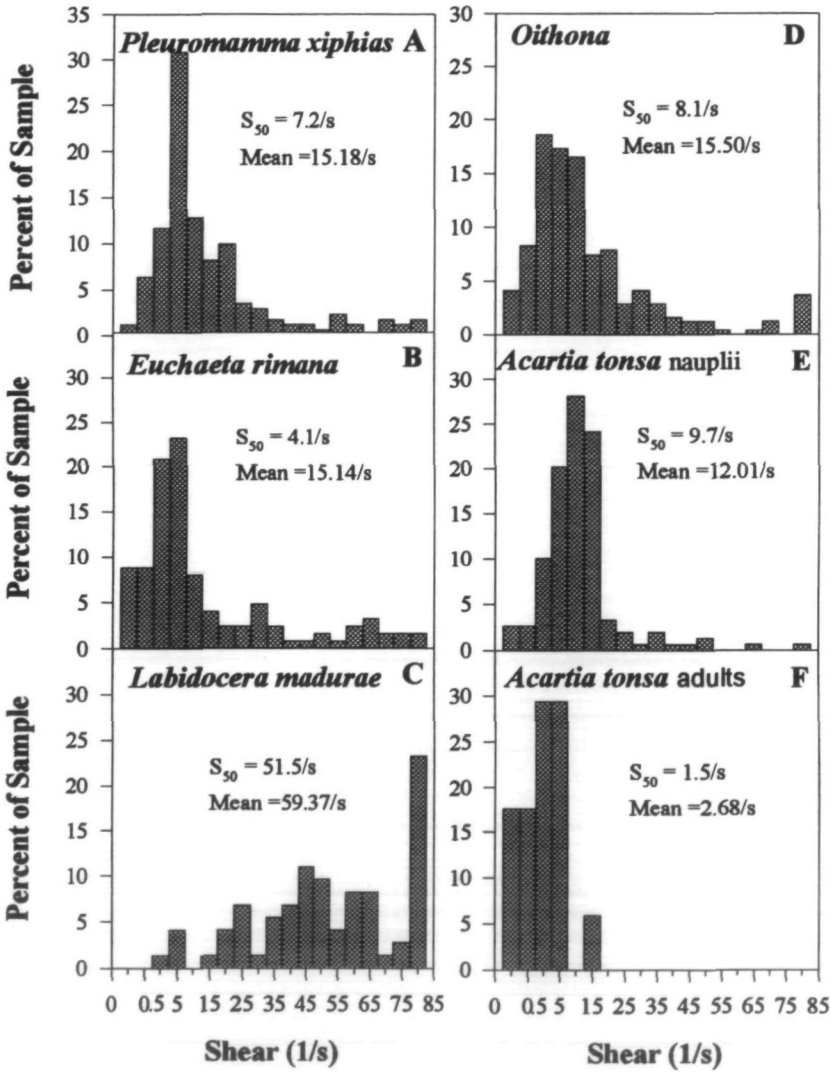

Fig. 3. Distributions of escape thresholds for five species of copepods. Plates are labeled as in Figure 2. Bin values give maximum separation at values below one and then are given in increments of 5 s^{-1}. The values at which 50% of animals had escaped (S_{50}), along with the mean value for all the escapes, are reported.

an S_{50} of 7.2 s^{-1} and *A.tonsa* nauplii had an S_{50} of 9.2 s^{-1}. The copepod with the largest S_{50} was *L.madurae* with a value of 50.2 s^{-1}. For this animal, <10% of the escapes occurred at a shear value of <20 s^{-1}.

Results of the Mann–Whitney *U*-test (Table II) show that the distributions of the escape reaction of *A.tonsa* adults and *L.madurae* were significantly different from each other and from the two other species tested ($P < 0.01$ for *A.tonsa* and $P < 0.001$ for *L.madurae*). The data show *A.tonsa* to be behaviorally the most

Table II. Results of the Mann–Whitney *U*-test for the differences between the distribution of escapes for the different species and developmental stage tested. Levels of significance are $*P < 0.05$; $**P < 0.01$; $***P < 0.001$. The Mann–Whitney statistic is shown in parentheses

	Size	*E.rimana*	*P.xiphias*	*L.madurae*	*Oithona*	*A.tonsa* adult	*A.tonsa* nauplii
E.rimana	3.0	–	–	–	–	–	–
P.xiphias	5.0	* (8903)	–	–	–	–	–
L.madurae	2.5	*** (1150)	*** (11 149)	–	–	–	–
Oithona	0.8	ns (16 709)	ns (19 827)	*** (1939)	–	–	–
A.tonsa adult	0.8	** (74 391)	*** (2447)	*** (1224)	*** (3220)	–	–
A.tonsa nauplii	0.15	** (1500)	ns (12 317)	*** (10 082)	ns (16 885)	*** (2162)	–

sensitive species tested, while *L.madurae* was the least reactive species. *Pleuromamma xiphias*, *Oithona* and *A.tonsa* nauplii could not be distinguished by their distribution of escape responses. *Euchaeta rimana* was found to be significantly different from both *P.xiphias* ($P = 0.004$) and *A.tonsa* nauplii ($P = 0.004$), but was not found to differ from *Oithona* ($P = 0.09$). Based on these results, the animals can be organized in terms of behavioral sensitivity, progressing from the most to least sensitive as *A.tonsa* adults (1.5) > *E.rimana* (4.1) > *P.xiphias* (7.2) = *A.tonsa* nauplii (9.7) = *Oithona* (8.1) > *L.madurae* (51.1).

Discussion

In Fields and Yen (1996), the fluid mechanical signal which elicited the escape reaction in *P.xiphias* was characterized. Fluid shear was found to be the least variable characteristic eliciting the escape reaction and best explained the pattern of escape surrounding the siphon. In this study, the escape thresholds of four other oceanic species (*E.rimana*, *Oithona*, *L.madurae* and *A.tonsa*) were determined. We tested the hypothesis that different species, and different age groups within a species, will have distinct thresholds needed to elicit an escape reaction. We suggest that these differences may form the basis for selective predation. Historically, research in the field of selective feeding has proceeded in two parallel directions. Initially, much attention was given to the body-size predation hypothesis outlined by Brooks and Dodson (1965). The prey's predation risk was accessed solely by its relative size compared with other potential prey. A second avenue examined the prey's behavioral characteristics in an effort to understand how behavior altered the predator's ability to perceive potential prey. This research includes the study of vertical migration patterns (Zaret and Suffern, 1976) and the effects of the motion of individual prey on their detectability (Horridge and Boulton, 1967; Ware, 1973). Both of these approaches have been aimed at the perceptive abilities of the predators. In this study, we develop an additional component for interpreting selective predation which considers the mechanoreceptive abilities of the prey. By comparing the shear thresholds needed to elicit an escape reaction for different copepod species, insights into the abilities of these animals to avoid particular predators can be predicted.

Signal detection

Shear is a measure of the change in velocity over space. The detection of shear, therefore, is maximized by sampling over a large spatial scale. Therefore, a bigger antennal span is expected to give rise to greater sensitivity in the animal. Yet, the results show that between species there appears to be little relationship between the span of the antennae and the escape threshold. *Acartia hudsonica* adults, one of the smaller animals tested (1.0 mm), were the most sensitive, while *L.madurae*, one of the larger animals, were the least sensitive. *Pleuromamma xiphias*, the largest animal (5 mm), had an intermediate threshold value. This is not to suggest that the span of the antennae does not contribute to the sensitivity of the animal; rather, these results suggest that other factors controlling the sensitivity may be more important when animals are from different environments. Within a species, size may be an important component determining the escape threshold. This is supported by *Acartia* nauplii which elicited escape reactions at an average shear value six times higher than the adult of the same species.

Model explaining threshold shear value

Virtually all copepods exhibit an escape reaction to an apparent predation risk. Based on the sensory abilities of copepods, it has been suggested that the escape reaction is a response to a threshold fluid mechanical disturbance (Strickler and Twombly, 1975; Haury *et al.*, 1980; Yen and Fields, 1992; Fields and Yen, 1996). The intermediate values of the thresholds (Figure 3) suggest two opposing forces which determine the upper and lower limits of the magnitude of the stimulus needed to cause an escape reaction. The upper limit is probably defined by the risk of a delayed escape reaction. The strike efficiency of a predator commonly increases with decreased distance from its prey. Therefore, if a copepod's escape reaction is delayed, its risk of predation will increase as it is approached by the predator. The finality of an unsuccessful escape clearly has strong evolutionary repercussions on the individual and is expected to occupy a powerful position in shaping the timing of the escape reaction.

Less obvious, and more difficult to assess, are the conditions that give rise to an inhibition of the escape reaction at very low shear values. It is unlikely that the low number of escapes at very low shear values indicate a neurophysiological threshold defined by the animal's mechanoreceptors. Fluid mechanical disturbances become neurological impulses through the motion of one or several of the numerous mechanoreceptive setae that adorn the antennae of many copepods (Strickler and Bal, 1973; Yen *et al.*, 1992). Neurophysiological results suggest that individual mechanoreceptors of copepods can detect fluid displacements as small as 10 nm at frequencies up to 1000 Hz (Yen *et al.*, 1992) and fluid velocities as low as 20 $\mu m\ s^{-1}$. If eliciting the earliest escape reaction possible was the primary factor determining the threshold at which prey initiate an escape reaction, then, based on a 10 nm displacement theshold, copepods would elicit an escape response at the slightest stimulus. This would include escaping from stimuli created by a potential predator and to water motion such as those found

in normal turbulent regimes. This clearly was not the case in this study for any of the animals tested. This indicates that the behavioral threshold is higher than the neurophysiological data suggest.

There are several possible explanations to account for the inhibition of the escape reaction at low shear values. The escape reaction incurs an energetic cost on the copepods which can consume up to 400 times the normal energetic expenditure (Strickler, 1975; Alcaraz and Strickler, 1988; Marrase *et al.*, 1990). This was supported by field studies (Kils, 1989) which showed that repeated escape reactions exhaust copepods to the point that they become easier prey for juvenile herring. Secondly, unnecessary escape reactions have been shown to increase the predation risk by attracting the attention of both visual (Bryan, 1973; Ware, 1973; Zaret, 1980) and mechanoreceptive predators (Horridge and Boulton, 1967). An additional consequence of the rapid escape response is the increased encounter rate with predators due to the higher swimming speeds (Rothschild and Osborn, 1988). As a result, the escape threshold of the prudent copepod would be a function of the risk of predation due to a delayed escape reaction and the cost and risk of an unnecessary escape (Figure 4).

The degree of behavioral sensitivity is in part a reflection of the ambient water motion characteristic of the animal's environment. If the animal is not adapted/habituated to the background shear values, it will exhibit an inordinate number of unnecessary escape reactions. Different oceanic habitats have, on average, different degrees of background shear motion which can cause inappropriate escape. Therefore, copepods captured from different habitats may differ in the threshold values needed to elicit the escape. We compared the escape

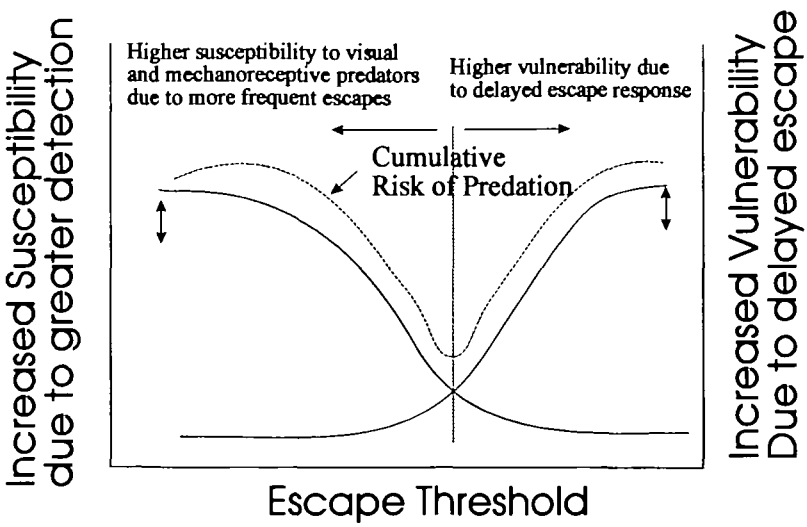

Fig. 4. The proposed relationship between the risk of a delayed escape reaction and the incurred risks and costs of an unnecessary escape reaction. High thresholds are curtailed by the higher vulnerability due to a delayed escape reaction, while low thresholds are limited by the metabolic costs and increased delectability as a result of numerous excess escape reactions.

thresholds of the five species tested here to literature values for shear found in each of their habitats.

Critical shear values relative to ambient water motion

Energy dissipation rates (ε) vary spatially and temporally. Measured values of ε in the ocean vary from 10^{-2} W kg^{-1} in tidal channels to 10^{-9} W kg^{-1} in deep pelagic environments (Lazier and Mann, 1989), resulting in a Kolmogoroff length scale (η; Lazier and Mann, 1989) ranging from 0.6 to 36 mm, respectively (Table III). Thus, while feeding, the oceanic copepods examined in this study can be considered to operate on length scales below η and, therefore, are exposed to laminar shear fields. An exception to this may be copepods found in tidal channels and shallow bays where η can be <1 mm.

To estimate shear within microscale eddies caused by natural turbulence, fluid motion was considered to be expressed as linear isotropic shear. The mean shear rate (S) was calculated as (Lazier and Mann, 1989):

$$S = \left(\frac{\pi\varepsilon}{10\upsilon}\right)^{1/2}$$

assuming a ratio of observed eddies to Kolmogoroff eddies of 20.

Among the copepods examined, the threshold values consistently exceeded average ambient values. In addition, the magnitude of the threshold qualitatively reflects the energetic values found in the environment (Figure 5). *Euchaeta rimana*, which resides in relatively quiet waters, required a relatively low shear value to initiate an escape reaction. In contrast, *L.madurae*, which were captured in highly energetic waters, required shear values an order of magnitude greater. *Pleuromamma xiphias* and *Oithona* required intermediate values to initiate the escape.

The threshold shear value for adult *A.tonsa*, the lowest for all the species tested, was surprising in light of their environment. Their extremely low threshold suggests that they reside in hydrodynamically quiet environments, which is in stark contrast to the presumably tumultuous nature of the estuarine environment. As suggested in Figure 4, the timing of the escape reaction is a balance of risk of predation and the costs of an unnecessary escape. Threshold values for *A.tonsa* are likely dominated by the high degree of predation pressure suffered by these

Table III. Average dissipation rate and Kolmogoroff scale for the environmental condition of the species tested

Location	Representative species	ε (W kg^{-1})	Kolmogoroff scale (mm)	Environmental shear (s^{-1})	Reference
Tidal channel		10^{-2}	0.65	54.78	Wesson and Gregg, 1994
Shallow bays	*L.madurae*	10^{-3}	1.16	17.32	Estimated
Surface coastal	*Oithana*	10^{-5}	3.66	1.73	Gargett *et al.*, 1984
Estuarine	*A.tonsa*	10^{-6}	6.5	0.54	Estimated
Surface pelagic	*E.rimana*	10^{-7}	11.56	0.17	Mann and Lazier, 1991
Deep pelagic	*P.xiphias*	10^{-9}	36.57	0.02	Yamazaki and Kamykowski, 1991

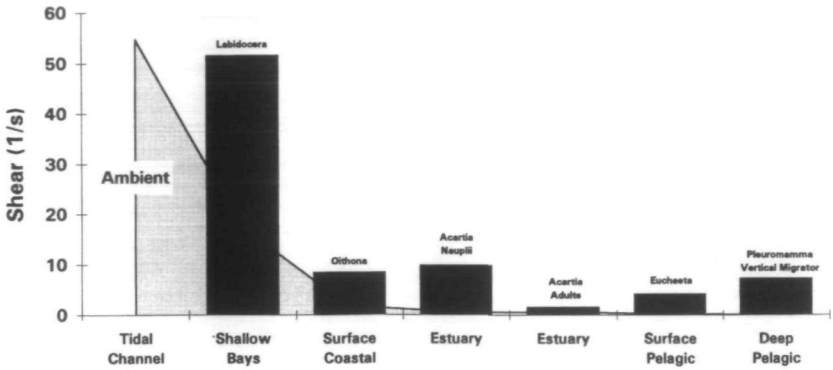

Fig. 5. Escape thresholds for the copepod species tested with respect to the literature values for average environmental shear rates. Environmental shear rates are given in Table III.

animals (Lonsdale, 1981). Predation has been proposed to regulate the abundance of *Acartia* in a small temperate lagoon (Landry, 1976). The high predation pressure on *Acartia* [Lonsdale (1981) and references therein] explains the lower threshold needed to elicit the escape reaction. In situations where animals suffer a high risk of predation, evolutionary selection clearly favors successful escapes over conserving the energy associated with an unnecessary escape.

Between species and within a single species of copepods, variability in escape behavior can help explain observed patterns of prey selection. Animals with limited abilities to detect predators remotely may be more susceptible to predation even if their escape speeds and accelerations are adequate to escape certain predators. This explanation offers an alternative explanation to that posed by Greene and Landry (1988) who suggested that the decreasing vulnerability of the older developmental stages of *Calanus pacificus* to predation was the result of the greater escape ability of the larger animals. Their conclusion presupposes that the behavioral sensitivity of *C.pacificus* remains constant with ontogeny. The results of this study, which compares the escape thresholds of adult and nauplii *A.tonsa*, suggest that the behavioral threshold of the nauplii is higher. Therefore, it is not only that the nauplii are slower at escaping than the adults, but it is also that they do not escape at the same distance from the predators as do the adults, which may make them more susceptible to predation.

The degree of variability in the threshold shear value is critical to understanding its effect on selective predation under different environmental conditions. The latter aspect was discussed by Hwang (1991) where it was demonstrated that the calanoid copepod *Centropages hamatus* can habituate to different levels of fluid disturbances and hence alter its threshold for an escape reaction. During the 'sensitive phase' which occurred during the transition from calm to turbulent motion, animals were found to exhibit numerous escape reactions at relatively low thresholds. With time, however, the critical value needed to elicit the escape reaction increased to a steady value. As a result, some plasticity in the behavioral threshold can be expected and may change the relative sensitivity of co-existing species.

It is apparent that selective predation on a single species can be explained by prey body size (Werner and Hall, 1974; Confer and Blades, 1975) or visibility (Zaret, 1975; Zaret and Kerfoot, 1975); however, it has been shown to be inadequate in explaining feeding preference in mixed populations (Drenner *et al.*, 1978) or in populations including different developmental classes. Differential escape thresholds and escape abilities offer likely explanations. To date, little is known about the relationship between the neurophysiology of the animal and its behavioral response. Part of the problem is that copepods are not single-sensor animals, but rather possess numerous sensors and types of sensors which are integrated on some level prior to eliciting a behavior response. Sensory integration allows for the threshold needed to elicit an escape reaction to be modified by background levels of chemical signals (Dodson, 1988; Watson and Hessinger, 1989; M.Brewer, personal communication). It is likely that future studies on the behavioral sensitivities of different zooplankton species will provide a better understanding of the mechanisms of feeding by selective marine planktivores.

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