

Escape strategies in co-occurring calanoid copepods

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Abstract

We show how four co-occurring calanoid copepod species modulate their responses to two contrasting hydrodynamic stimuli. Species-specific patterns in escape behavior included quantitative differences in performance to each stimulus type. Using high-speed video, we compared escape reactions in *Acartia hudsonica*, *Centropages hamatus*, *Tortanus discaudatus*, and *Temora longicornis*. Responses to a flow field created by a suction tube involved reorientation away from the source of suction followed by a series of vigorous power strokes. Responses to brief computer-controlled hydrodynamic stimuli had short latencies (a few milliseconds) and consisted of a reorientation followed by a few pereopod power strokes. Two species responded to this stimulus with higher escape speeds. The other two species gave a larger response to the suction stimulus by producing long escape trajectories. Each species perceived the magnitude of the threat in a different way and employed a different strategy in the escape response.

Zooplankters are exposed to multiple predators, and strategies to decrease predation risk include small size, transparency, vertical migration, spines, bioluminescent discharges, and in the case of marine copepods, a rapid and strong escape response. Calanoid copepods comprise the most abundant metazoan plankton in the oceans and constitute a major trophic link in oceanic food webs. Calanoids respond to threats with spectacular escape responses, reaching speeds of 500 to 1,000 body lengths per second (e.g., Strickler 1975; Buskey et al. 2002). This capability plays an important role in their successful evasion of predators (e.g., Drenner et al. 1978; Viitasalo et al. 1998) and hence in their numerical success in the oceans. The motor performance underlying these escapes is among the highest reported in any animal group (Lenz and Hartline 1999; Lenz et al. 2004).

Escape responses can be elicited by both hydrodynamic (Hartline et al. 1999; Kiørboe et al. 1999; Lenz and Hartline 1999) and photic stimuli (Buskey et al. 1986, 1987; Buskey and Hartline 2003). Escape jumps have been studied cinematographically (Strickler 1975; Buskey et al. 2002) and as force output (Svetlichnyy 1987; Alcaraz and Strickler 1988; Lenz and Hartline 1999). The escape consists of a short latency (2 to 10 milliseconds in response to a hydrodynamic stimulus; Buskey et al. 2002), followed by the retraction of the cephalic appendages (Alcaraz and Strickler 1988; Lenz et al. 2005) and a reorientation of the body axis (Buskey et al. 2002; Buskey and Hartline 2003).

All of this occurs within a few milliseconds and is followed by the metachronal sequence of pereopod power strokes (Alcaraz and Strickler 1988; Buskey et al. 2002; Lenz et al. 2004). Often escapes are composed of multiple sets of power strokes by the pereopods, which are repeated at a rate of 50 to 200 Hz (Lenz and Hartline 1999; Buskey et al. 2002; Lenz et al. 2004). Escape performance in terms of reaction times, appendage movements, force production, and the time-course of repeated power strokes during escapes has been examined in tethered copepods (*Cyclops scutifer*: Strickler 1975; Alcaraz and Strickler 1988; *Calanus helgolandicus*: Svetlichnyy 1987; *Undinula vulgaris*: Lenz and Hartline 1999; *Pleuromamma xiphias*: Hartline et al. 1999; *Calanus finmarchicus*: Lenz et al. 2004, 2005). Turning movements and whole-body trajectories in response to predator-mimic stimuli have been studied in free-swimming animals using high-speed video (e.g., Buskey et al. 2002; Buskey and Hartline 2003; Waggett 2005). These studies suggest that copepods can modulate their escape response depending on the type of threat.

Species-specific differences in escape behavior have been demonstrated in calanoids (Viitasalo et al. 1998; Lenz et al. 2000; Buskey et al. 2002) but have not been studied systematically. Studies on the feeding habits of predators have suggested that some copepods are preyed upon preferentially by certain predators (e.g., Hopkins et al. 1996; Purcell and Decker 2005). Thus, species-specific differences in startle responses may be important in determining the outcome of individual predator-prey encounters (Waggett and Buskey 2006, 2007). Survival of an encounter with a predator depends on a copepod's sensitivity in detecting the presence of the predator (including its attack), its reaction time, the speed of its escape, as well as direction and distance of escape trajectory. Here, we present comparative data on escape responses in four calanoid species from different families within the same superfamily (Centropagoidea). The four coastal species, *Acartia hudsonica*, *Temora longicornis*, *Tortanus discaudatus*, and *Centropages hamatus* have widely overlapping distributions and thus presumably

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Table 1. Lengths and aspect ratios for the four species of copepod studied. Estimated maximum errors due to out-of-plane trajectories are indicated. Some escapes extended beyond the field of view. Sample size in parentheses.

	<i>Tortanus</i>	<i>Centropages</i>	<i>Acartia</i>	<i>Temora</i>
Total length (mm)	1.54 ± 0.08 (13)	1.24 ± 0.11(12)	1.01 ± 0.11(21)	0.74 ± 0.11(4)
Prosoma length (mm)	1.22 ± 0.06 (13)	0.99 ± 0.08(15)	0.75 ± 0.06(22)	0.59 ± 0.07 (16)
Prosoma aspect ratio	2.4	2.5	2.6	1.8
Cylinder: aspect ratio error (%)	10	21	14	5
Tube: aspect ratio error (%)	12	15	15	7
Accepted offscreen jumps				
Bar	2 (26)		1 (25)	
Suction	0 (17)	1 (6)	4 (15)	8 (18)

encounter similar threats from predators. Escapes were elicited by two types of hydrodynamic stimulus, one that mimicked a steady flow field set up by a predator and one that mimicked the rapid pounce of a predatory attack.

Materials and Methods

Collection, maintenance, and identification of copepods—Calanoid copepods were collected daily in June and July from Frenchman Bay off Mount Desert Island (44°25.7'N, 66°11.8'W), Maine, by towing a 0.5-m-diameter net (333- μ m mesh) at 10–15-m depths. Adult females and C5s were sorted by species (*Acartia hudsonica*, *Tortanus discaudatus*, *Centropages hamatus*, and *Temora longicornis*), either into 1.75-liter jars or directly into experimental aquaria, and maintained at collection temperatures (12–15°C). In sorting free-swimming animals, individuals were identified by size, swimming characteristics, pigmentation, and phototactic behavior. After each experiment, animals were preserved for later identification under a dissecting microscope. Mean prosoma and total lengths for the animals used in the experiments are given in Table 1.

Experimental setup—The basic setup for the behavior experiments has been described elsewhere (Buskey et al. 2002; Buskey and Hartline 2003). Groups of individuals (5 to 15) were transferred into the experimental chamber (dimensions: 2.5 cm wide \times 8.3 cm long \times 5 cm high; Fig. 1), which was filled nearly to the top with filtered (Whatman glass fiber; model GF/C) cool seawater. For temperature control, the chamber was placed in a cooling jacket (dimensions: 5.7 cm wide \times 10.5 cm long \times 5.7 cm high) through which cold freshwater from an ice bath was circulated using a peristaltic pump. The jacket was covered with black paper except for view channels for the video cameras and illumination. The view channels were covered with red gelatin filter material (Wratten 25, Edmund Scientific) since copepods are known to be relatively insensitive to long wavelengths of light (Buskey et al. 1989; Cohen and Forward 2002). An acrylic cover excluded light from above except for a rectangular window matching the aquarium profile that was covered with opal glass. The opal glass was illuminated uniformly from above with a Dolan-Jenner model 3100 Fiber Lite[®] illuminator, which provided light intensities of 60–95 μ mol photons

$\text{m}^{-2} \text{s}^{-1}$ just below the glass. Experimental temperature was monitored with a digital thermometer (YSI, Inc. model 4600) and kept within 2°C of collection values. The chambers rested on a vibration-isolated bench-top (Newport Model BT-2024).

Hydrodynamic stimuli—Two types of stimuli were employed, a “pounce mimic” and a “flow-field mimic.” The pounce mimic stimulus consisted of a 3-mm-diameter plastic cylindrical bar spanning the width of the chamber and attached by a rod to a piezoelectric transducer (Burleigh PZL-060, Exfo), which was computer driven (Fig. 1; Gassie et al. 1993). The rapid vertical movement of this bar produced a hydrodynamic disturbance that decayed with distance following dipole equations (Kundu 1990; Buskey et al. 2002):

$$u_r = a^2 U \cos(\theta) / r^2 \quad (1)$$

$$u_\theta = a^2 U \sin(\theta) / r^2 \quad (2)$$

$$A = -2a^2 U / r^3 \quad (3)$$

which describe the radial (u_r) and tangential (u_θ) components of fluid movement, and the fluid deformation rate (A) as functions of bar radius (a), bar movement (U), distance from the bar axis (r), and angle with respect to the line of movement (θ). Stimulus waveforms were generated by a personal computer (Sony PCG-F420) running LabVIEW 5.1 with output to the D/A converter of a DAQPad 6070E (National Instruments) driving the piezoelectric amplifier (Fig. 1). The stimulus used in these experiments was a trapezoidally modulated 1.5-cycle sine wave with 700-Hz frequency and a maximum vertical excursion of the cylinder of 34.4 μ m and peak velocity of 88 mm s^{-1} (Buskey et al. 2002). The time from half-peak to peak deformation rate was thus 0.24 ms. This stimulus form generates the high-frequency waveform components to which an animal must be sensitive in order for rapid reactions to occur.

Flow-field-mimicking stimuli were generated using a steady suction applied to a Pasteur pipette with bore diameter 1.4 mm centered in the experimental aquarium (Fields and Yen 1997; Viitasalo et al. 1998; Kiørboe et al. 1999). A flow rate of $\sim 0.85 \text{ mL s}^{-1}$ was generated with

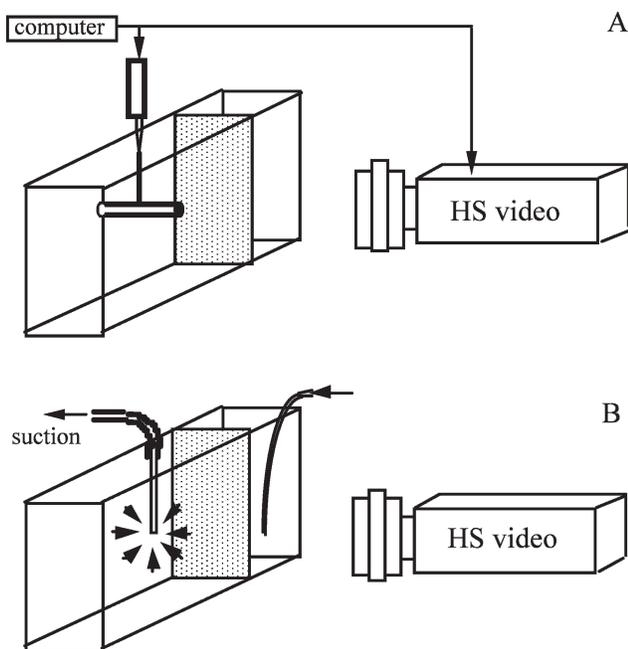


Fig. 1. Diagram of stimulus and filming setups. (A) Bar stimulus: escape responses were generated by rapid movements of a plastic cylinder under computer control. (B) Suction stimulus: escapes were produced when the copepod was drawn sufficiently close to the orifice of a suction tube. A mesh window divided the chamber into two compartments. A cotton filter was fitted into the right compartment for the suction stimulus. Arrows indicate direction of water flow.

a peristaltic pump, and it sufficed to elicit escapes within a few millimeters of the orifice. The hydrodynamic disturbance created was calculated from:

$$u_r = V/(4\pi r^2) \quad (4)$$

$$\Delta = -V/(2\pi r^3) \quad (5)$$

where V is the flow rate in the pipette, and r is the distance from the orifice. The “rise time” for deformation rate to reach a given level was defined as the time to achieve that level from half, which equaled $1/(3\Delta)$ for the suction stimulus. These calculations were validated by tracking neutrally buoyant *Artemia* cysts entrained in the flow field. Error in computed Δ owing to the walls and surface of the experimental chamber were calculated to be small ($<10\%$ for all but the most distant (>9 mm) start points. Water removed from the experimental aquarium was recirculated through a cotton-plug filter that smoothed and distributed the flow evenly to minimize currents in the main chamber. At the screen separating the filter from the remaining chamber, flow rates were <1 mm s^{-1} , resulting in a very low deformation rate superimposed on the suction flows eliciting escapes.

Data recording and analysis—Video recording: Behavior of the animals was recorded at 1,000 frames per second (shutter speeds of 0.001 to 0.0003 s) with a high-speed video camera (Kodak Motioncorder Analyzer Model SR-

3000) equipped with a 50-mm f1.4 Nikon Nikkor lens, and stored on VCR tapes. The area viewed was $\sim 17 \times 20$ mm, depending somewhat on experiment type (26×31 mm in the later half of suction-tube experiments owing to greater trajectory lengths). For the bar stimulus, the line of view coincided with the axis of the cylinder, and the two-dimensional position of any individual in the field sufficed to allow calculation of the water movement experienced by the animal. The stimulus and video recording were synchronized to the nearest 1 ms, and data were recorded for 0.3 s prior and for 0.7 to 1 s after the stimulus was activated. The trigger signal from the stimulus “marked” the frame following the signal as the time-origin ($t = 0$) for the video sequence. Times assigned to the video frames by the camera were thus randomly delayed up to 1 ms.

Analysis: Video records were reviewed to select escape paths suitable for motion analysis. Since escape trajectories were recorded in two dimensions, only those copepods with escape jumps perpendicular to the line of view to the camera were suitable for detailed analysis. Whether this condition was met for a given clip was determined by computing the aspect ratio of length to width of the copepod image just prior to and during the escape. Trajectories were accepted if this was within 30% of the actual aspect ratio for the species (determined by microscope). On average, this resulted in underestimates of true trajectory parameters of $\sim 10\%$ (Table 1). The escape sequences of accepted trajectories were captured by computer and analyzed using National Institutes of Health (NIH) Image software (Wayne Rasband, <http://rsb.info.nih.gov/nih-image/>). Reorientation occurring in the first few milliseconds of the response was quantified using the NIH Image angle tool to determine the angle of the body with respect to either the center of the stimulus object or a horizontal reference line just prior to and just after the turn. Trajectories were quantified starting with the video frame preceding the onset of movement. Coordinates for the center of gravity for a copepod image were digitized in successive frames, from which jump distances, velocities, and accelerations for tabulation, statistics, and plotting were derived. Statistical tests were performed following Siegel (1956).

Results

Escape trajectories varied among species and between stimuli—Figure 2 shows a series of superimposed images taken at 5-ms intervals of an escape by a *Tortanus discaudatus* triggered by the brief movement of the bar seen end-on in the lower left corner. The initial movement is a reorientation that started prior to 5 ms and was completed by 10 ms, resulting in a turn of almost 90° away from the bar. The turn is followed shortly by a single power-stroke sequence by the thoracic pereopods. The animal moved at least three body lengths in under 20 ms in this relatively weak response. While the reorientation and pereopod power strokes were typical components of the response, the presence, absence, and magnitude of the turn

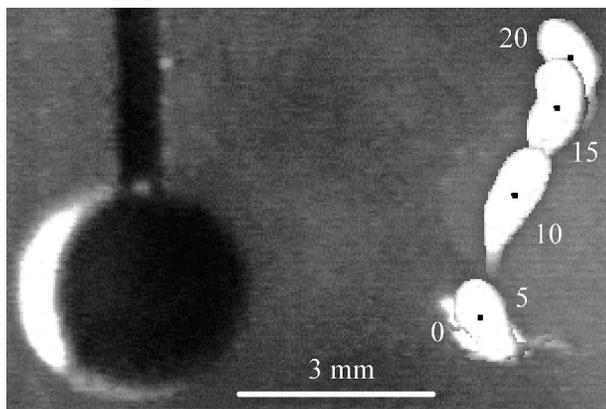


Fig. 2. Escape to the pounce-mimic stimulus showing superimposed images of a copepod (*Tortanus discaudatus*) at 5-ms intervals following the abrupt movement of the 3-mm cylindrical bar seen on the left. Note the initial reorientation upward, followed by acceleration (during pereiopod power stroke) and deceleration (after completion of power stroke and during return stroke) in this single-“kick” escape. Pereiopods cannot be seen in this sequence. Black square on the image of the animal indicates center of gravity, which was used to determine the escape trajectory. The peak cylinder velocity used to trigger this escape was 8.8 cm s^{-1} , which computes to a movement of $\sim 4 \text{ cm s}^{-1}$ of the animal or a water deformation rate of 17 s^{-1} .

as well as the number of power strokes produced in the response were dependent on stimulus type and species.

Representative escape trajectories for all four species and both bar (Fig. 3A,C,E,G) and suction (Fig. 3B,D,F,H) stimuli are shown in Fig. 3. While there was substantial variation in the form and orientation of the individual trajectories, some general patterns emerged. *Tortanus* tended to produce long escape trajectories to both types of hydrodynamic stimuli, perhaps in part owing to the fact that it was the largest species tested. *Centropages* and *Temora* produced shorter trajectories to the bar than to the suction, whereas *Acartia* responded with relatively short escapes to both types of stimulus. Trajectories tended to be linear, but in the longer ones, sharp mid-trajectory turns were occasionally observed. In addition to the differences in trajectory lengths, the figure shows suggestions of differences in the reaction points and the orientation of trajectories. These qualitative species and stimulus-specific differences in escape patterns are analyzed quantitatively in the measurements presented in the following sections.

Temora was markedly less sensitive to the bar stimulus than were other species—The sudden movement of the bar, mimicking the hydrodynamic signals produced by a predatory pounce, elicited escape responses in a majority of the individuals of all species except *Temora*, provided they were close enough to the bar. The percentage of animals responding decreased with distance from the bar (Fig. 4A). The distance at which 50% responded serves as a measure of behavioral sensitivity. This distance was between 6 and 7 mm for three species (Table 2), but it was less than 3 mm for *Temora*. The latter species, in fact, was so insensitive

that its 50% response distance could not be determined reliably owing to the lack of response in animals even practically touching the bar. Computed mean threshold deformation rate was an order of magnitude greater for *Temora* than it was for the other species (15 s^{-1} vs. $\sim 1.5 \text{ s}^{-1}$; Table 2).

Tortanus was markedly more sensitive to the suction stimulus than were other species—Most copepods drawn into the flow field surrounding the suction pipette escaped successfully ($\sim 8\%$ were “captured” by the tube). Because the reactions were monitored only in two dimensions, the measured distances from the orifice at which escapes were initiated on average were somewhat underestimated (10%, see Methods). The cumulative probability of a reaction as a function of distance for the four species is shown in Fig. 4B, which presents the fraction of animals escaping (ordinate) at and beyond the distance given by the value of the abscissa. Species-specific averages for these distances are given in Table 3. For *Acartia*, *Centropages*, and *Temora*, median reaction distances were not significantly different from each other ($p > 0.20$, median test), and 50% reaction distances were near 4 mm, where the computed water deformation rate was $\sim 2 \text{ s}^{-1}$ (Eq. 5; Table 3). *Tortanus*, however, initiated escapes at significantly greater distances ($p < 0.001$, median test), with computed threshold deformation rates an order of magnitude smaller (0.2 s^{-1}). These mean deformation rates are all smaller (sensitivities are greater) than the corresponding ones for the bar, and two species (*Tortanus* and *Temora*) were markedly more sensitive to the suction tube than to the bar (Tables 2, 3). While 90% of *Acartia* and *Temora* escaped to deformation rates just under 80 s^{-1} , this level of responsiveness was achieved at much lower levels by *Centropages* (5 s^{-1}) and *Tortanus* (2 s^{-1}).

There were no significant interspecies differences in reaction time to hydrodynamic stimuli—For the pounce-mimic stimulus, the time from stimulus delivery to the first detectable movement was measured to the nearest millisecond. The mean reaction times for the four species, all around 3 ms, are given in Table 2. None differed significantly from the others ($p > 0.5$, median test). Reaction times for the suction tube could not be obtained because there was no defined timing point to use as a reference.

Larger species tended to produce greater peak velocities—Escape velocities (speeds) were high, with velocities typically reaching peaks of 150 to 600 mm s^{-1} during the first or second power-stroke sequence. Figure 5 shows the time-course of velocity for typical responses to the bar (Fig. 5A) and suction (Fig. 5B) stimuli for *Tortanus*. Escape velocities over time were characterized by multiple peaks, which corresponded to individual sets of power strokes (two for the bar and three for the suction stimulus in this figure). Both species-specific and stimulus-type differences in escape velocities were observed (Fig. 5; Tables 2, 3). Maximum escape velocities were significantly different among species (bar: $p < 0.001$; suction: $0.001 < p < 0.01$, median test, two-tailed). To the bar stimulus,

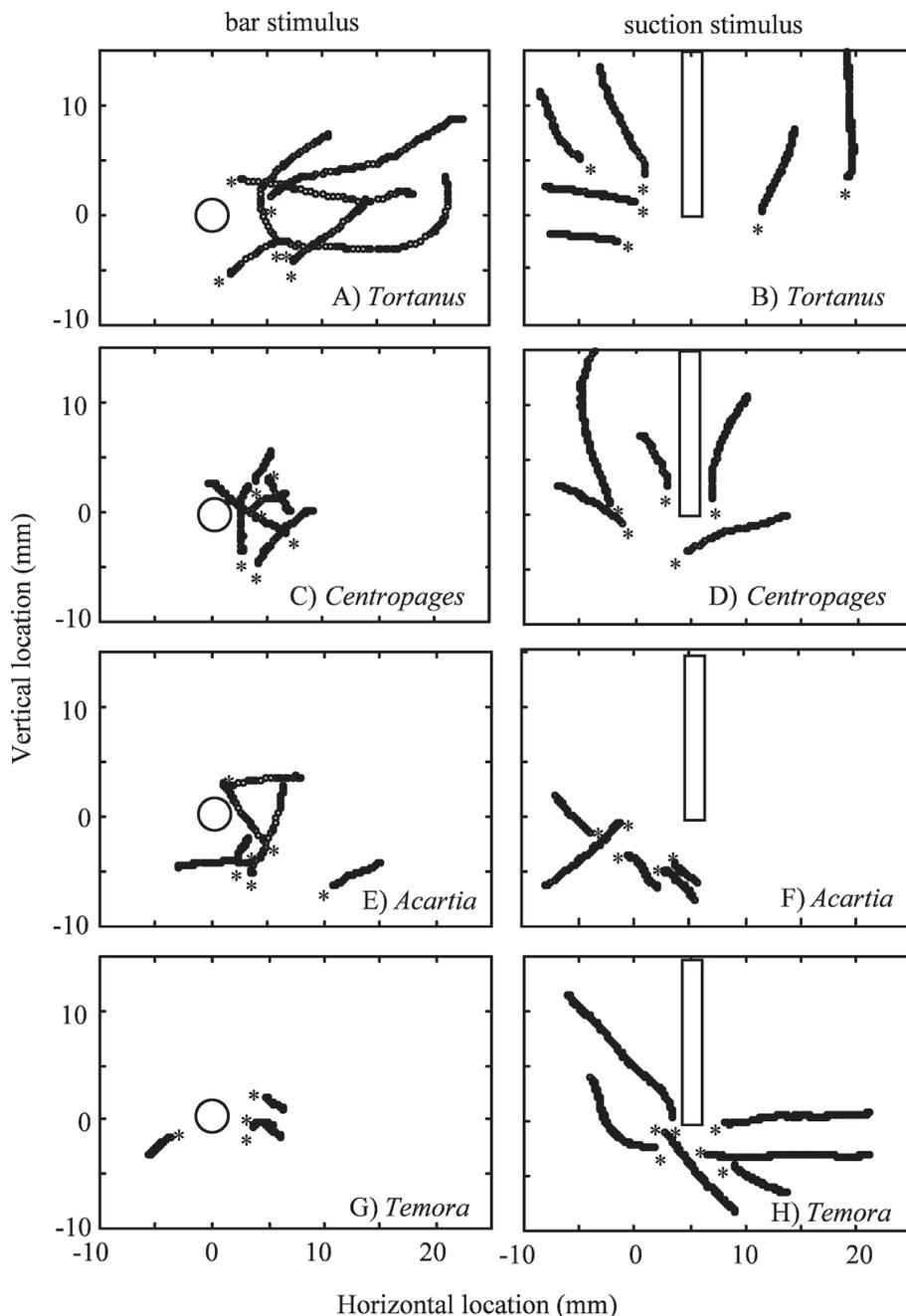


Fig. 3. Escape trajectories for four species of calanoid responding to two hydrodynamic stimuli. (A,C,E,G) Escape trajectories in response to an abrupt, brief, $34\text{-}\mu\text{m}$ movement of a cylindrical bar (bar stimulus); bar location is indicated by large open circle. (B,D,F,H) Escape trajectories in response to a suction tube with a flow rate of 0.85 mL s^{-1} (suction stimulus); location of suction tube is indicated by the open vertical bar. Asterisks (*) indicate the position at time of initiation of the escape.

Tortanus produced the highest velocities ($>500\text{ mm s}^{-1}$), *Centropages* and *Acartia* were intermediate, and *Temora* produced the lowest velocities (200 mm s^{-1} ; Table 2). To the suction stimulus, *Centropages* and *Tortanus* responded with similar maximum velocities (350 and 343 mm s^{-1} , respectively). *Acartia* escaped with maximum velocities near 300 mm s^{-1} (Table 3), and *Temora* showed maximum velocities near 250 mm s^{-1} (Table 3).

Maximum escape velocities in response to the two hydrodynamic stimuli differed for some species. *Tortanus* responded to the suction stimulus with lower escape velocities ($p < 0.0001$, Mann–Whitney *U*-test, two-tailed; Tables 2, 3) and lower accelerations ($p < 0.05$, Mann–Whitney *U*-test, two-tailed; Tables 2, 3) than to the bar. *Acartia* also responded with lower peak escape velocities to the suction stimulus ($0.002 < p < 0.02$, Mann–Whitney *U*-

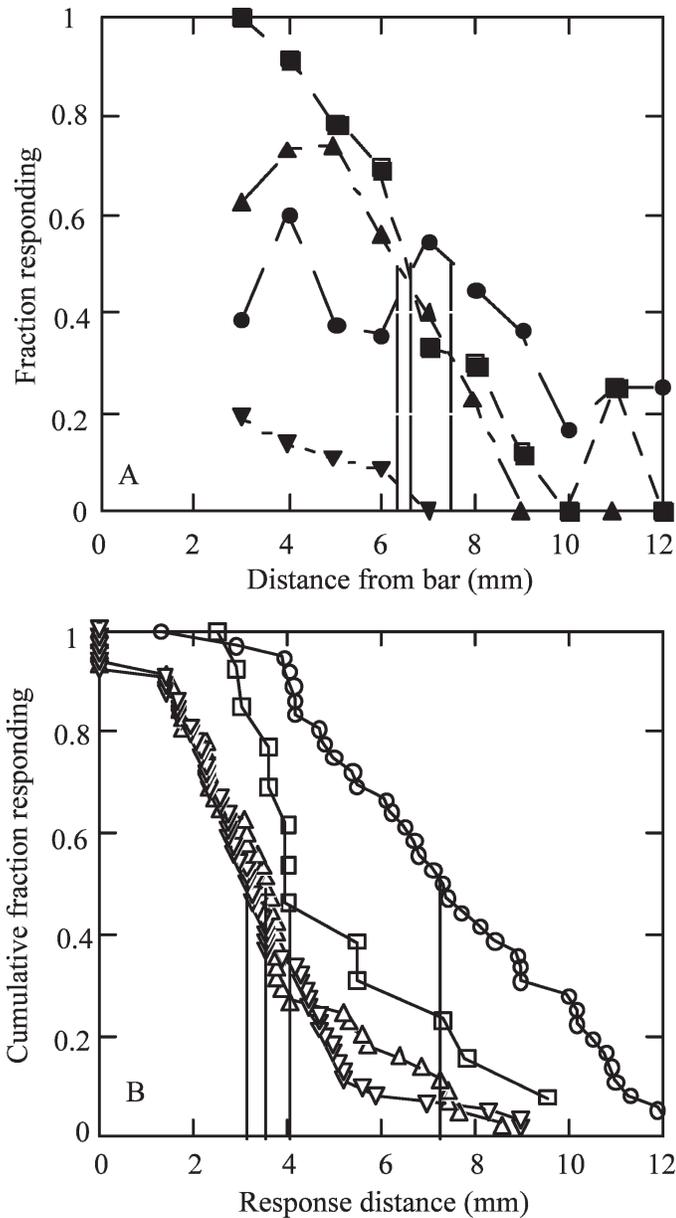


Fig. 4. Probability of an escape response as a function of distance from stimulus. (A) Bar stimulus: points plotted are the fraction of the number of individuals of a given species producing escapes to the total number of individuals at the same distance from the center of the cylinder (1-mm bins). (B) Suction stimulus: ordinate of each point is the cumulative fraction of escapes triggered at the distance given by the abscissa; points at $x = 0$ represent animals "captured" by the suction tube. Vertical lines indicate the 50% escape distance for each species. Circles: *Tortanus discaudatus*; squares: *Centropages hamatus*; triangles: *Acartia hudsonica*; inverted triangles: *Temora longicornis*.

test, two-tailed; Tables 2, 3), although maximum accelerations were not significantly different ($p > 0.10$, Mann-Whitney U -test, two-tailed; Tables 2, 3). Maximum escape velocities and accelerations in the other two species were similar for the two stimuli (no significant difference, $p > 0.10$, Mann-Whitney U -test, two-tailed; Tables 2, 3).

There were striking differences among species in the magnitude of response to bar and suction stimuli—The cumulative distance traveled during escapes for the various species is shown in Fig. 6. The slopes of the plotted lines give the average velocities during the escapes, and the end point of each line indicates the gross displacement (ordinate) and the duration (abscissa) of that escape. Escapes consisted of one to more than ten kicks (sets of power strokes). Each kick is associated with a high velocity region, corresponding to the power stroke, and a short period of deceleration, corresponding to the return stroke, which results in the undulating pattern shown in Fig. 6A (inset). Note that many escapes are characterized by less vigorous kicks at the end of the escape trajectory, leading to a smaller displacement during the last kick (Fig. 6, bar stimulus: *Centropages*, *Acartia*, *Temora*).

Escape responses to the bar stimulus were typically short, lasting 50 ms or even less, and distances jumped ranged from less than 5 mm to over 15 mm (Fig. 6). The median escape distance to the bar stimulus was 6.3 mm, and species-specific differences in escape distances were significant (median test, $0.02 < p < 0.05$, two-tailed). *Temora* displayed the shortest escape jumps to the bar stimulus (2.3 mm, Table 2), and *Tortanus* displayed the longest (9 mm, Table 2). These escapes were characterized by a small number of kicks, or sets of pereopod power strokes. The number of kicks for *Tortanus*, *Temora*, and *Centropages* were similar ($p > 0.10$, $df = 2$, median test). *Acartia* responded with a larger number compared to the other three species ($0.01 < p < 0.02$, $df = 3$, median test). Escape responses to the suction stimulus were longer in duration (50 to over 150 ms) and in distances jumped (Fig. 6). The median distance jumped to the suction stimulus was 8.1 mm, and there were no significant differences in escape distances among the four species (median test, $0.20 < p < 0.30$, two-tailed).

The escape trajectories of *Acartia* and *Tortanus* to the two hydrodynamic stimuli were similar in length ($p > 0.10$, Mann-Whitney U -test); mean distances jumped are shown in Tables 2 and 3. In contrast, *Temora* and *Centropages* responded to the two stimuli with significantly different jump distances (*Temora*: $p < 0.002$, *Centropages*: $0.02 < p < 0.05$; Mann-Whitney U -test, two-tailed). The difference in jump distance was associated with a significantly greater number of kicks in response to the suction (*Centropages*: $0.01 < p < 0.02$, *Temora*: $0.02 < p < 0.05$; median test, one-tailed).

Distances jumped did not depend on the distance between the animal and the stimulus and, thus, were not related to stimulus strength. Correlation coefficients were not significant ($p > 0.05$, Spearman rank). In tethered calanoids (*Undinula vulgaris*), Lenz and Hartline (1999) reported an increase in pereopod power strokes with stronger stimuli. The free-swimming copepods in these experiments did not have a fixed orientation with respect to the stimulus. Thus, owing to inferred directional sensitivities of the sensory receptors to the fluid flow past the first antenna (Weatherby and Lenz 2000; Fields et al. 2002), there is likely to have been more variability in effective

Table 2. Escape parameters for abrupt hydrodynamic stimulus (bar). Response distance indicates distance that 50% of individuals responded with an escape (Fig. 4A). Mean \pm SD, numbers in parentheses indicate sample size (n).

	<i>Tortanus</i>	<i>Centropages</i>	<i>Acartia</i>	<i>Temora</i>
Response distance (mm)	7.0	6.5	6.1	<3
Deformation rate at response distance (s^{-1})	1.2	1.4	1.7	>15
Latency (ms)	3.1 \pm 0.6 (22)	2.8 \pm 0.5 (20)	3.1 \pm 0.5 (15)	2.8 \pm 0.5 (4)
Total distance jumped (mm)	9.0 \pm 4.5 (18)	4.5 \pm 1.7 (16)	5.8 \pm 2.4 (13)	2.3 \pm 0.5 (4)
Max. velocity ($mm\ s^{-1}$)	536 \pm 57 (21)	386 \pm 28 (9)	387 \pm 100 (14)	262 \pm 28 (4)
Max. acceleration ($mm\ s^{-2}$)	197 \pm 52 (21)	160 \pm 43 (8)	166 \pm 48 (14)	124 \pm 54 (4)
Sets of power strokes (No. of kicks)	2.0 \pm 1.1 (21)	1.7 \pm 1.0 (21)	3.1 \pm 1.3 (14)	1.5 \pm 0.6 (4)
% of escapes with initial turns	27 (15)	53 (17)	35 (17)	100 (5)
Mean turn angle (degrees)	57 \pm 6 (4)	84 \pm 37 (9)	103 \pm 27 (6)	96 \pm 65 (4)

stimulus intensity in this free-swimming situation. A similar result was found by Buskey et al. (2002) for two other species of *Acartia*.

Strength of escape was modulated by either changing the distance jumped or by changing escape velocities—Figure 7 shows how the escape responses to the two hydrodynamic stimuli clustered in different combinations of distance jumped and escape velocity for each species. For *Centropages*, maximum escape velocities varied little with distance jumped, and there were shorter escape distances to the bar than to the suction stimulus. This difference in distances jumped to the two types of stimuli was even more pronounced for *Temora*, where all escapes in response to the bar were much shorter than to the suction. In *Tortanus* and *Acartia*, escape velocities correlated with distance jumped. In both species, escape distances to the two stimuli overlapped.

Variability in jump direction and species-specific differences decreased predictability for escape response—Reorientation by the copepod prior to the escape jump achieved both a greater distance from the stimulus and provided an element of unpredictability to the escape. Turning was observed in $\sim 45\%$ of escape responses (bar: 44%, $n = 54$; suction: 46%, $n = 41$). Turns preceded the pereopod power strokes and took approximately 2 to 4 ms. The fraction of escapes with turns ranged from 15% to 100%, where both the highest and the lowest percent occurred in *Temora*. Species-specific differences in the probability of turning were significant (bar: $0.01 < p < 0.02$; suction: $0.02 < p < 0.05$; $df = 3$, chi-square for k-independent samples).

Tortanus turned with greater frequency to the suction stimulus than to the bar ($p < 0.0004$, Fisher Exact-Probability test), and *Temora* turned more frequently to the bar stimulus ($p < 0.0025$, Fisher Exact-Probability test). *Centropages* and *Acartia* showed no difference in turning frequency between stimulus types ($p \geq 0.30$, Fisher Exact-Probability test).

In general, the escape trajectories in these calanoids tended to be upward. *Tortanus* and *Centropages* swam upward in response to both bar and suction stimuli (*Tortanus*: 90% upward, $p < 0.01$; *Centropages*: 80% upward, $0.02 < p < 0.05$; two-tailed, chi-square test). *Acartia* responded by swimming upward to the bar (70% up, $0.02 < p < 0.05$; two-tailed, chi-square test), but not to the suction stimulus (50% up). *Temora* swam upward to the suction stimulus (75% up, $0.02 > p > 0.05$; two-tailed, chi-square test), and down in response to the bar (100% down; not significant, binomial test).

The most efficient escape would maximize the distance between the copepod and the source of the disturbance. This trajectory is represented in Fig. 8 by the diagonal drawn with a slope = 1, where the jump distance (x -axis) equals the displacement from the stimulus (escape efficiency = 100%). The data points plot the individual escapes to the bar and to the suction stimuli for the four species. The preponderance of escapes carried the copepods away from the threat (points above the axis). To the suction stimulus, turns redirected the individual animals away from the stimulus (*Tortanus*: $p < 0.001$; *Temora*: $p < 0.005$; two-tailed, chi-square test; *Acartia*: $p = 0.016$; *Centropages*: $p = 0.11$; two-tailed, binomial test). All four species optimized their escape trajectories (Fig. 8), with overall escape

Table 3. Escape parameters for slowly intensifying hydrodynamic stimulus (suction). Response distance indicates mean distance of initiation of an escape (Fig. 4B). Mean \pm SD, numbers in parentheses indicate sample size (n).

	<i>Tortanus</i>	<i>Centropages</i>	<i>Acartia</i>	<i>Temora</i>
Response distance (mm)	7.3 \pm 2.8 (36)	4.9 \pm 2.2 (13)	3.8 \pm 1.9 (41)	3.7 \pm 1.8 (56)
Deformation rate at response distance (s^{-1})	0.34	1.2	2.2	2.7
Rise time at response distance (s)	1.0	0.28	0.15	0.12
Total distance jumped (mm)	7.8 \pm 2.6 (15)	11.0 \pm 5.5 (6)	4.6 \pm 2.0 (5)	10.7 \pm 4.1 (16)
Max. velocity ($mm\ s^{-1}$)	343 \pm 112 (15)	367 \pm 55 (6)	289 \pm 80 (10)	244 \pm 57 (16)
Max. acceleration ($mm\ s^{-2}$)	158 \pm 39 (15)	187 \pm 43 (6)	136 \pm 37 (10)	145 \pm 44 (16)
Sets of power strokes (No. of kicks)	2.8 \pm 0.8 (15)	4.2 \pm 2.5 (6)	3.5 \pm 1.6 (15)	7.6 \pm 2.5 (18)
% of escapes with initial turns	69 (16)	67 (3)	44 (9)	15 (13)

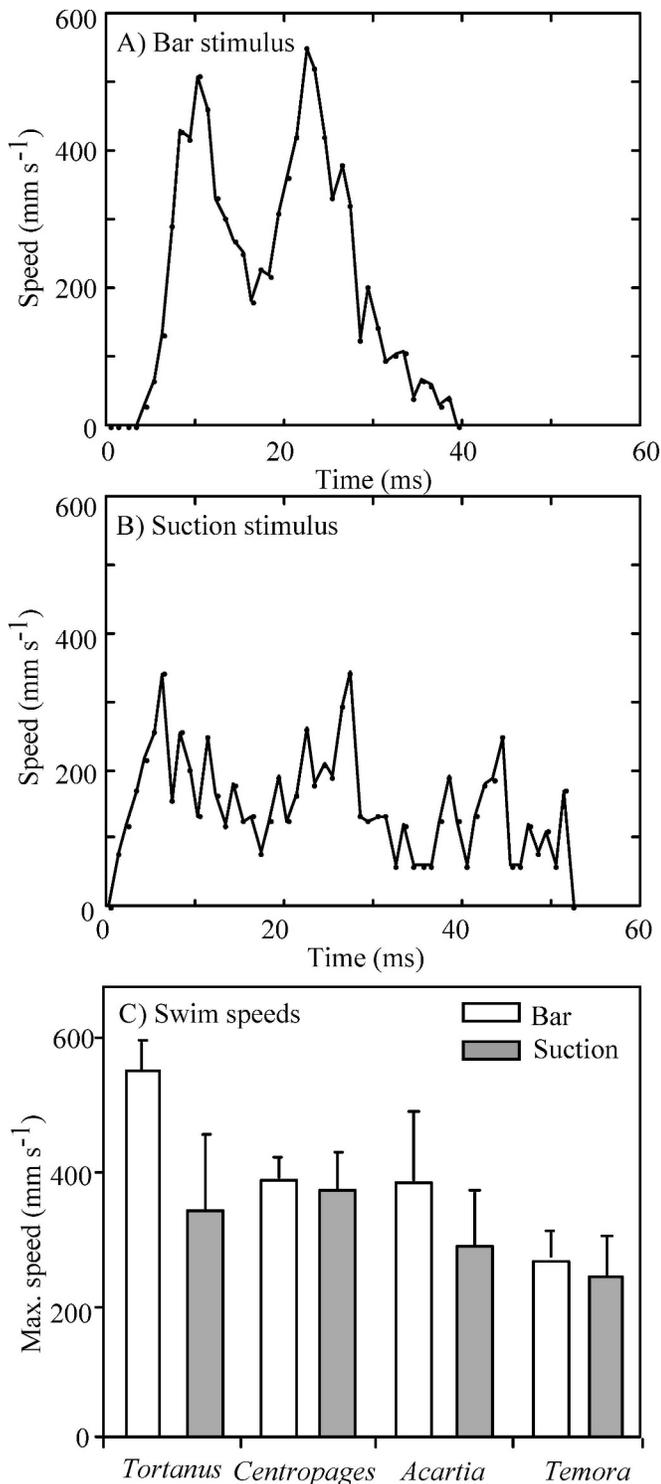


Fig. 5. Swimming speeds for *Tortanus discaudatus* over time during an escape in response to (A) the bar and (B) the suction stimulus. Swimming speeds were measured at 1-ms intervals. (C) Average maximum swim speeds during escapes from the bar and suction stimulus for four species.

efficiencies of over 80% (*Temora*: 88%; *Acartia*: 83%; *Tortanus*: 82%; *Centropages*: 78%). In contrast, escapes to the bar stimulus were highly variable (Fig. 8), and turns were not significantly away from the stimulus (*Centropages* and *Temora*, binomial test; *Tortanus* and *Acartia*, chi-square test). Average escape efficiencies were lower (*Tortanus*: 51%; *Acartia*: 34%; *Centropages*: 27%). Interestingly, the direction of *Temora*'s escapes were similar to both types of stimuli (escape efficiency to bar: 87%), although this species was relatively non-responsive to the bar stimulus and responded with short jumps.

Discussion

Pelagic communities are characterized by multiple predators foraging on multiple prey species. Omnivory is pervasive, and the complexity of the biological interactions defies theoretical treatments of these ecosystems. Typically, predator-prey models have focused on encounter rates to predict predation risk (e.g., Gerritsen and Strickler 1977; Rothschild and Osborn 1988; Mann et al. 2006). These models underestimate the importance of behavior in predator-prey outcomes, and thus they may have only limited predictive value (e.g., Sih et al. 1998; Lima 2002). Calanoid copepods lower their predation risk through behavior, such as vertical migration (e.g., Iwasa 1982; Bollens and Frost 1989) and the startle response (e.g., Trager et al. 1994; Suchman and Sullivan 1998; Clarke et al. 2005). However, the effectiveness of the copepod escape response varies with ontogeny (Greene and Landry 1985), predator type (Suchman and Sullivan 1998; Viitasalo et al. 1998; Waggett and Costello 1999), and prey species (Viitasalo et al. 1998; Waggett 2005). The present analysis suggests that escape responses are modulated as a function of stimulus, and that copepod species perceive and respond to threats in different ways.

Behavioral responsiveness—Published values of behavioral sensitivity to water deformation rates range from $<0.5 \text{ s}^{-1}$ to $>10 \text{ s}^{-1}$ in calanoid copepods (Kjørboe et al. 1999; Buskey et al. 2002; Titelman and Kjørboe 2003). Our results suggest that this range may reflect species- and stimulus-specific differences in sensitivity. In the current study, all four species were more sensitive to the slowly increasing deformation rates (suction). However, relative sensitivities to the two types of stimuli ranged from very similar (*A. hudsonica*) to five times more sensitive (*T. discaudatus* and *T. longicornis*). The two stimuli represent two extremes, and the hydrodynamic signals produced by most predators will be in between. For example, in our experiments, *A. hudsonica* reacted at strain rates $>0.6 \text{ s}^{-1}$ to the bar (rise time = 0.24 ms) and $>0.3 \text{ s}^{-1}$ to the suction (rise time = 1,000 ms). Heuch et al. (2007) reported behavioral thresholds at strain rates $>0.5 \text{ s}^{-1}$ to a salmon head cast approaching *Acartia* at 16 cm s^{-1} (rise time = 40 ms). This corresponded to a detection distance of 1.5 cm from the fish head. At 0.5 mm ahead of the first antenna of a swimming copepod (*Euchaeta antarctica*), Catton et al. (2007) measured strain rates on the order of 10 s^{-1} , which

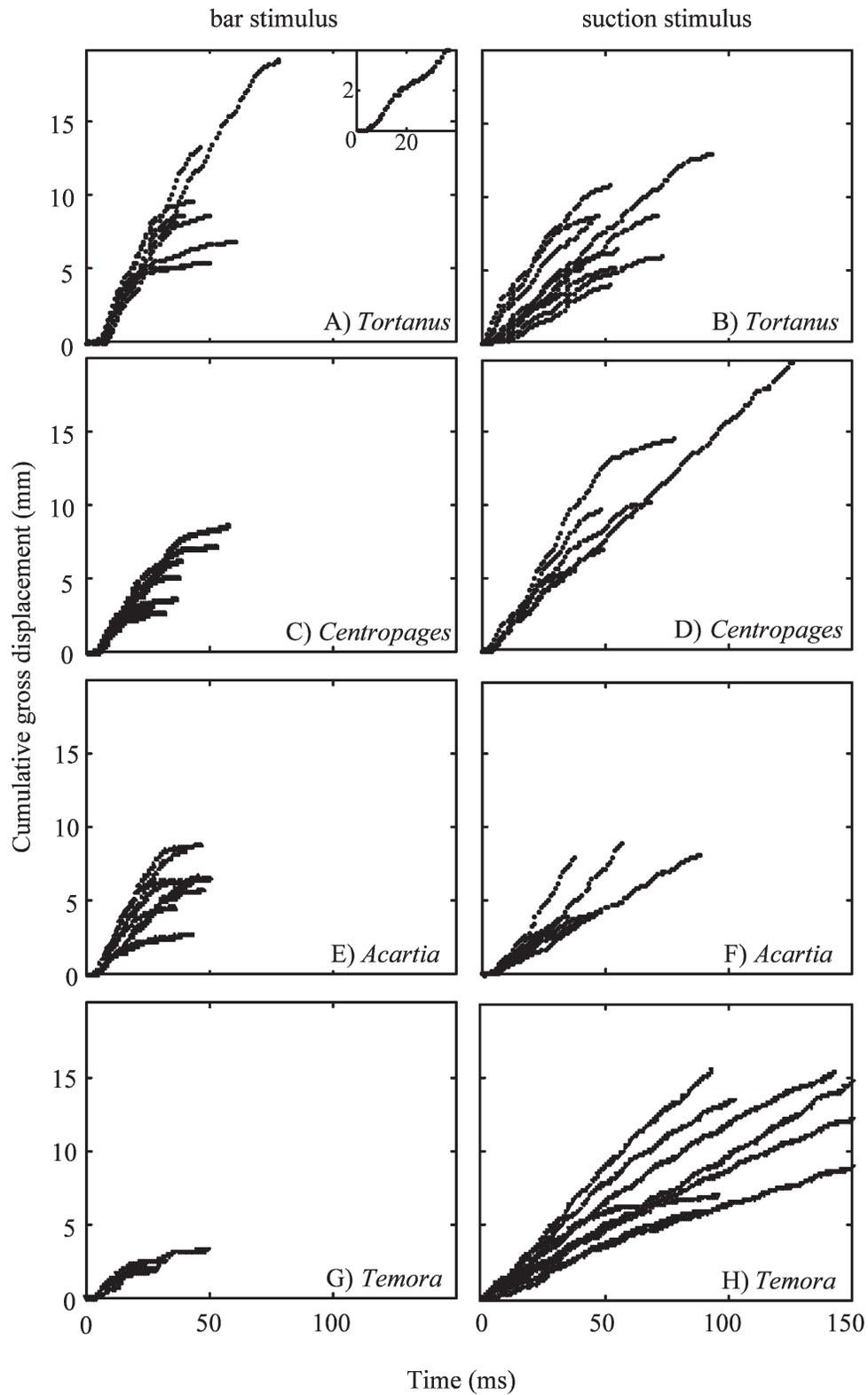


Fig. 6. Gross displacement over time in escape responses to (A,C,E,G) bar stimulus and (B,D,F,H) suction stimulus for the four species. Inset in (A) shows the trajectory for a single escape for the first 40 ms. Gross displacement was measured at 1-ms intervals from the beginning of the stimulus for the bar ($T = 0$) and first detectable escape movement for the suction.

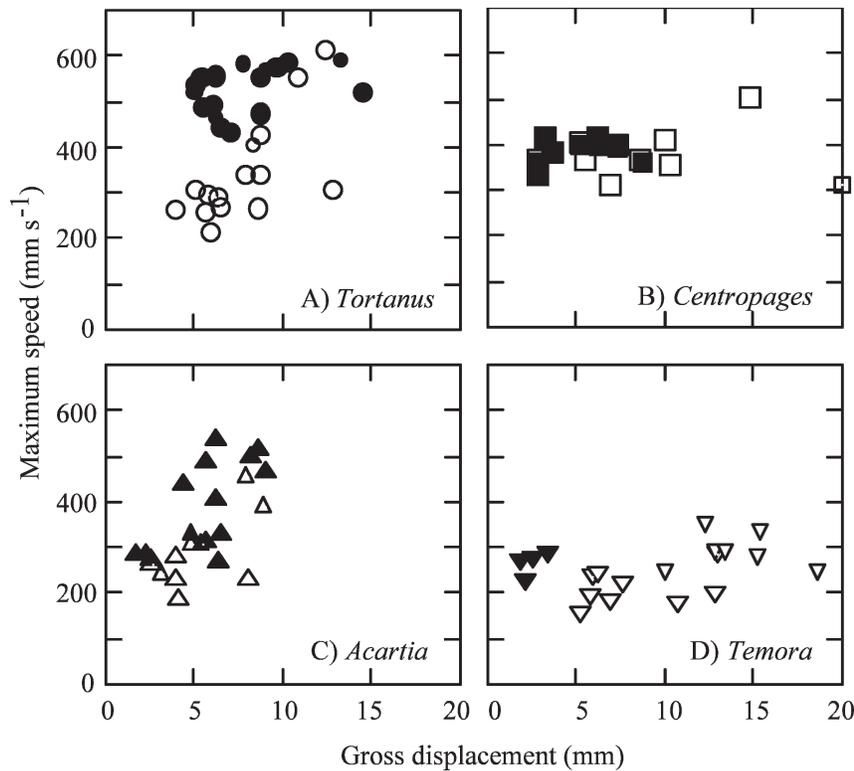


Fig. 7. Gross displacement vs. maximum escape speeds for the two stimuli (bar: closed symbols; suction: open symbols) and four species: (A) *Tortanus discaudatus*; (B) *Centropages hamatus*; (C) *Acartia hudsonica*; and (D) *Temora longicornis*. Smaller symbols indicate displacements produced by individuals that swam offscreen.

are 4 to 20 times greater than the average deformation rates that elicited escapes to our stimuli.

Speed—Maximum swim velocities scale with organism length to the two-thirds power (Fig. 9A; Domenici and Blake 1997; Lenz et al. 2004). Based on relatively few measurements (Lenz et al. 2004), swimming performance in copepods appears to also follow a two-third power relationship, but they are offset by nearly an order of magnitude above the relationship established for the fishes (Fig. 9A). Mean escape velocities measured in the current study scaled to copepod size provide an indicator of relative performance (Fig. 9A,B). Escape velocities for *Centropages* and *Temora* to both hydrodynamic stimuli fell on the regression line (Fig. 9B). However, escape velocities in *Acartia* and *Tortanus* were greater than expected to the bar stimulus (Fig. 9B), suggesting that these two species adjust their escape velocities to the threat. Waggett and Buskey (2007) found that *Temora turbinata* and *Paracalanus parvus* escaped at much higher escape velocities to a predatory fish attack than to an artificial stimulus.

Distance—In an effective escape, the distance jumped should remove the prey from the predator's detection field and/or flow field. This distance will vary with the sensory detection system (visual vs. mechanosensory) and hunting strategy (filter feeding, ambush, cruising) of individual predators. Flow fields to entrain prey are generated by many predators, such as gelatinous zooplankton (Sullivan

et al. 1997; Waggett and Costello 1999), some predatory copepods (Landry 1978; Yen and Fields 1992), barnacles (Trager et al. 1994), and mussels (Green et al. 2003). Prey entrained in the flow field of such a predator should jump sufficiently far to avoid becoming entrained again. The suction stimulus mimics aspects of a flow-field-generating predator. Two of the species tested, *Temora* and *Centropages*, responded to suction with long escapes that removed them from the flow field. The jumps of the smallest species, *Temora*, were as long as those of the two largest species, *Centropages* and *Tortanus* (Table 3; Fig. 10). *Temora*'s long trajectories were produced by long trains of pereopod power strokes (significant larger number of kicks than the other three species, $p < 0.001$, $df = 3$, median test). *Tortanus* responded to the suction stimulus with shorter jumps than to the bar. However, because of this species' behavioral sensitivity to this stimulus, the escape jumps were sufficiently long to remove individuals from the flow field. *Acartia* responded with the shortest jumps, and individuals from this species were often re-entrained in the flow field. This is consistent with the observation that ctenophores, such as *Mnemiopsis leidyi*, are more effective predators on *Acartia* than on *Temora* (Waggett and Buskey 2006).

Ambush predators detect their prey either visually (fish) or mechanoreceptively (chaetognaths, predatory copepods). Near-field hydrodynamic signals decay rapidly with distance (Kalmijn 1988), and even a short jump could remove the prey from the detection field of a mechan-

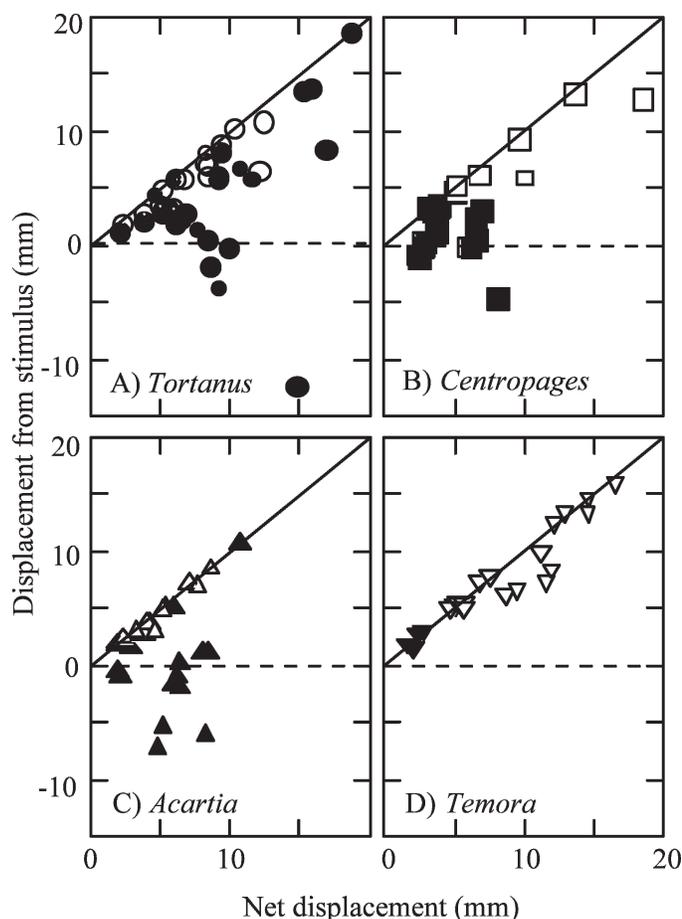


Fig. 8. Efficiency of escape trajectory: increase in distance from stimulus (y-axis) vs. net displacement from starting point (x-axis). Forty-five degree slope indicates escape trajectories directly away from stimulus and thus represents an efficiency of 100%. The dashed horizontal line indicates that the escape did not increase the distance between the organism and the stimulus. Points represent data for individual escapes (bar: closed symbols; suction: open symbols), and four species: (A) *Tortanus discaudatus*; (B) *Centropages hamatus*; (C) *Acartia hudsonica*; and (D) *Temora longicornis*. Smaller symbols indicate displacements produced by individuals that swam offscreen.

osensory predator. Temperate bays, such as Frenchman Bay, are often turbid, and the small and nearly transparent calanoid copepods may be nearly invisible. Thus, the short jumps produced in response to the bar stimulus may be sufficient to remove these small copepods from the visual field of a predatory fish. However, detection distance increases with prey size (Confer and Blades 1975), and we observed an increase in escape trajectories with copepod size (Fig. 10).

Direction—Direction of the jump, another important factor for an effective escape, can potentially increase predation risk, instead of reducing it. For an organism with a simple nervous system, such as a calanoid copepod, the suction stimulus may be relatively easy to localize compared to other types of hydrodynamic stimuli. Thus, escapes to the suction stimulus led to trajectories that were

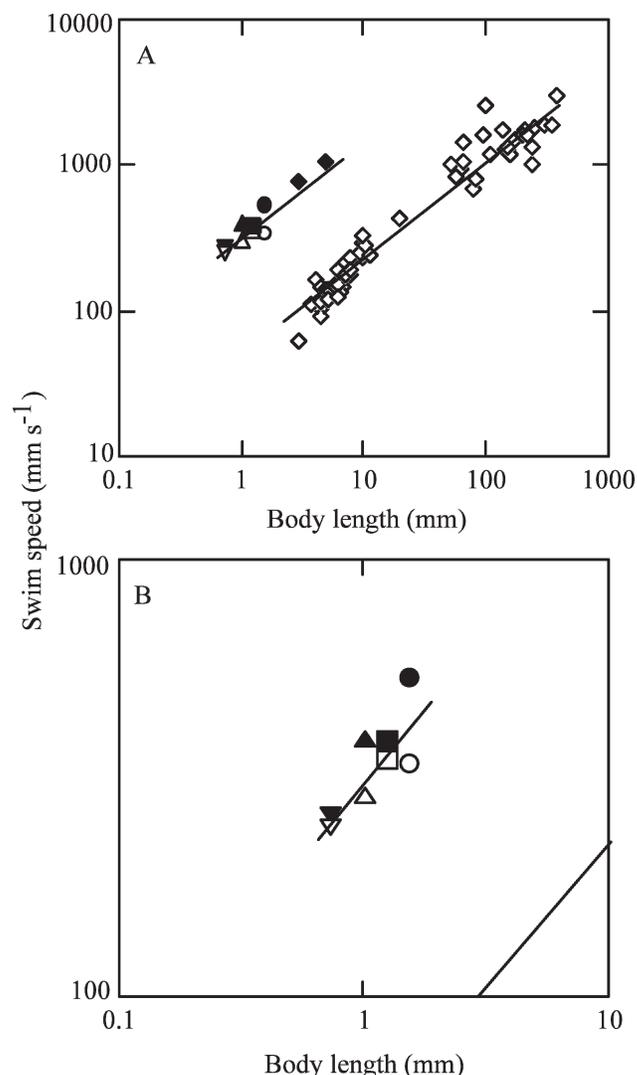


Fig. 9. (A) Maximum swim velocities scaled by organism length in response to the bar (closed symbols) and suction (open symbols) stimuli. Circles: *Tortanus discaudatus*; squares: *Centropages hamatus*; triangles: *Acartia hudsonica*; inverted triangles: *Temora longicornis*. Other symbols: open diamond: fishes (Domenici and Blake 1997; Shepherd et al. 2000; Williams et al. 1996); closed diamond: calanoid copepods (Lenz et al. 2004). Both solid lines indicate slope: $L^{2/3}$. (B) Maximum swim velocities measured in current experiment. Symbols are the same as in panel (A). Lines indicate slopes of $L^{2/3}$ drawn on the left for copepod and on the right for fish data.

nearly directly away from the stimulus (Fig. 8). However, not all species used the same strategy to achieve this. In three species, escapes jumps were preceded by a reorientation of the body axis (Table 3). In the fourth species, *Temora*, we observed a very low frequency of turns (15% of responses, Table 3), and reorientation appeared to have occurred during entrainment into the flow field prior to the initiation of an escape.

In contrast, the bar stimulus is very brief (stimulus duration: 1.5 ms), and behavioral responses are rapid (latencies: 2 to 3 ms). The accurate localization of such

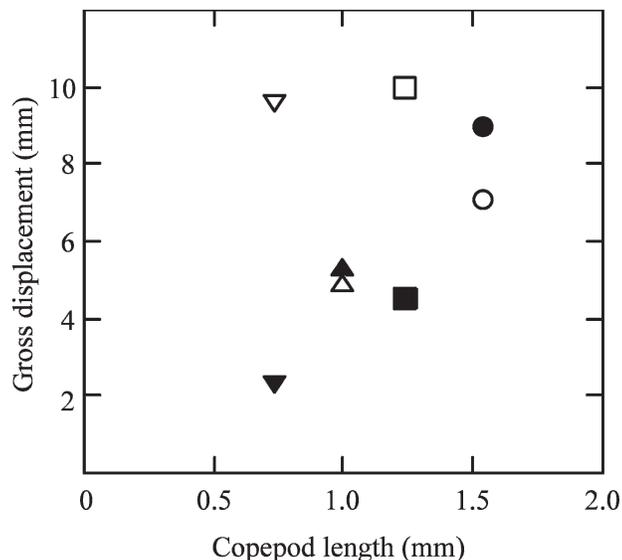


Fig. 10. Copepod length vs. mean escape distances in response to the bar (closed symbols) and suction (open symbols) stimuli. Circles: *Tortanus discaudatus*; squares: *Centropages hamatus*; triangles: *Acartia hudsonica*; inverted triangles: *Temora longicornis*.

a stimulus source would require a level of neural processing not expected in a crustacean. Nevertheless, escape jumps for three of the four species tested (*Tortanus*, *Centropages*, and *Temora*) were directed away from the stimulus, albeit trajectories were not optimized for maximizing distance between the animal and the stimulus. These escapes were characterized by high variability in the direction of the trajectory, which may increase the effectiveness of the escape. Once an attack is initiated, the predator commits to either attacking the prey's current position or to a strike at a predicted location. Thus, the prey's best strategy is to minimize predictability, and a change in swimming direction may be sufficient for a successful escape. In these experiments 27% to 100% of the escapes in response to the bar were preceded by a turn.

Behavioral ecology of predator evasion—Differences in swimming and foraging behaviors among copepods contribute to niche differentiation among pelagic copepods (Tiselius and Jonsson 1990; Paffenhöfer et al. 1996; Wiggert et al. 2005). Responses to predatory threats appear to be just as variable, and they add to the complexity of biological interactions in pelagic communities. A quantitative analysis of escape behavior in individual copepod species can start to establish which characteristics of the response are important in predicting the outcomes of specific predator–prey encounters. Recently, East Coast bays have experienced shifts in predators, which in turn have caused a major decline in *Acartia tonsa* populations (e.g., Purcell and Decker 2005; Costello et al. 2006). These changes might benefit other copepod species, which might be more effective in escaping from the ctenophore predator, *Mnemiopsis leidyi* (e.g., Waggett and Buskey 2006). In contrast, *A. hudsonica* escapes may be more effective against larval fishes, resulting in preferential feeding rates

on *Eurytemora affinis* (e.g., Shaheen et al. 2001). Thus, encounter rates are not sufficient to predict predator–prey outcomes in a community with multiple predators and prey. Changes in predator assemblages acting through differentials in escape strategy may have a cascading effect on community structure.

References

- ALCARAZ, M., AND J. R. STRICKLER. 1988. Locomotion in copepods: Pattern of movements and energetics of *Cyclops*. *Hydrobiologia* **167/168**: 409–414.
- BOLLENS, S. M., AND B. W. FROST. 1989. Zooplanktivorous fish and variable diel vertical migration in the marine planktonic copepod *Calanus pacificus*. *Limnol. Oceanogr.* **34**: 1072–1083.
- BUSKEY, E. J., K. S. BAKER, R. C. SMITH, AND E. SWIFT. 1989. Photosensitivity of the oceanic copepods *Pleuromamma gracilis* and *Pleuromamma xiphias* and its relationship to light penetration and daytime depth distribution. *Mar. Ecol. Prog. Ser.* **55**: 207–216.
- , AND D. K. HARTLINE. 2003. High-speed video analysis of the escape responses of the copepod *Acartia tonsa* to shadows. *Biol. Bull.* **240**: 28–37.
- , P. H. LENZ, AND D. K. HARTLINE. 2002. Escape behavior of planktonic copepods in response to hydrodynamic disturbances: High-speed video analysis. *Mar. Ecol. Prog. Ser.* **235**: 135–146.
- , C. G. MANN, AND E. SWIFT. 1986. The shadow response of the estuarine copepod *Acartia tonsa*. *J. Exp. Mar. Biol. Ecol.* **103**: 65–75.
- , AND ———. 1987. Photophobic responses of calanoid copepods: Possible adaptive value. *J. Plankton Res.* **9**: 857–870.
- CATTON, K. B., D. R. WEBSTER, J. BROWN, AND J. YEN. 2007. Quantitative analysis of tethered and free-swimming copepodid flow fields. *J. Exp. Biol.* **210**: 299–310.
- CLARKE, R. D., E. J. BUSKEY, AND K. C. MARSDEN. 2005. Effects of water motion and prey behavior on zooplankton capture by two coral reef fishes. *Mar. Biol.* **146**: 1145–1155.
- COHEN, J. H., AND R. B. FORWARD, JR. 2002. Spectral sensitivity of vertically migrating marine copepods. *Biol. Bull.* **203**: 307–314.
- CONFER, J. L., AND P. I. BLADES. 1975. Omnivorous zooplankton and planktivorous fish. *Limnol. Oceanogr.* **20**: 571–579.
- COSTELLO, J. H., B. K. SULLIVAN, AND D. J. GIFFORD. 2006. A physical-biological interaction underlying variable phenological responses to climate change by coastal zooplankton. *J. Plankton Res.* **28**: 1099–1105.
- DOMENICI, P., AND R. W. BLAKE. 1997. The kinematics and performance of fish fast-start swimming. *J. Exp. Biol.* **200**: 1165–1178.
- DRENNER, R. W., J. R. STRICKLER, AND W. J. O'BRIEN. 1978. Capture probability: The role of zooplankton escape in the selective feeding of planktivorous fish. *J. Fish. Res. Board Can.* **35**: 1370–1373.
- FIELDS, D. M., D. S. SHAEFER, AND M. J. WEISSBURG. 2002. Mechanical and neural responses from the mechanosensory hairs on the antennule of *Gaussia princeps*. *Mar. Ecol. Prog. Ser.* **227**: 173–186.
- , AND J. YEN. 1997. The escape behavior of marine copepods in response to a quantifiable fluid mechanical disturbance. *J. Plankton Res.* **19**: 1289–1304.
- GASSIE, D. V., P. H. LENZ, J. YEN, AND D. K. HARTLINE. 1993. Mechanoreception in zooplankton first antennae: Electrophysiological techniques. *Bull. Marine Sci.* **53**: 96–105.

- GERRITSEN, J., AND J. R. STRICKLER. 1977. Encounter probabilities and community structure in zooplankton: A mathematical model. *J. Fish. Res. Board Can.* **34**: 73–82.
- GREEN, S., A. W. VISSER, J. TITELMAN, AND T. KIØRBOE. 2003. Escape responses of copepod nauplii in the flow field of the blue mussel, *Mytilus edulis*. *Mar. Biol.* **142**: 727–733.
- GREENE, C. H., AND M. R. LANDRY. 1985. Patterns of prey selection in the cruising calanoid predator *Euchaeta elongata*. *Ecology* **66**: 1408–1416.
- HARTLINE, D. K., E. J. BUSKEY, AND P. H. LENZ. 1999. Rapid jumps and bioluminescence elicited by controlled hydrodynamic stimuli in a mesopelagic copepod, *Pleuromamma xiphias*. *Biol. Bull.* **197**: 132–143.
- HEUCH, P. A., M. H. DOALL, AND J. YEN. 2007. Water flow around a fish mimic attracts a parasitic and deters a planktonic copepod. *J. Plankton Res.* **29**(Suppl. 1): i3–i16.
- HOPKINS, T. L., T. T. SUTTON, AND T. M. LANCRAFT. 1996. The trophic structure and predation impact of a low latitude midwater fish assemblage. *Prog. Oceanogr.* **38**: 205–239.
- IWASA, Y. 1982. Vertical migration of zooplankton: A game between predator and prey. *Amer. Nat.* **120**: 171–180.
- KALMUN, A. J. 1988. Hydrodynamic and acoustic field detection, p. 83–130. *In* J. Atema, R. R. Fay, A. N. Popper and W. N. Tavolga [eds.], *Sensory biology of aquatic animals*. Springer.
- KIØRBOE, T., E. SAIZ, AND A. W. VISSER. 1999. Hydrodynamic signal perception in the copepod *Acartia tonsa*. *Mar. Ecol. Prog. Ser.* **179**: 97–111.
- KUNDU, P. K. 1990. *Fluid mechanics*. Academic.
- LANDRY, M. R. 1978. Predatory feeding behavior of a marine copepod, *Labidocera trispinosa*. *Limnol. Oceanogr.* **23**: 1103–1113.
- LENZ, P. H., AND D. K. HARTLINE. 1999. Reaction times and force production during escape behavior of a calanoid copepod, *Undinula vulgaris*. *Mar. Biol.* **133**: 249–258.
- , ———, AND A. D. DAVIS. 2000. The need for speed. I. Fast reactions and myelinated axons in copepods. *J. Comp. Physiol. A* **186**: 337–345.
- , A. E. HOWER, AND D. K. HARTLINE. 2004. Force production during pereopod power strokes in *Calanus finmarchicus*. *J. Mar. Systems* **49**: 133–144.
- , ———, AND ———. 2005. Temperature compensation in the escape response of a marine copepod, *Calanus finmarchicus* (Crustacea). *Biol. Bull.* **209**: 75–85.
- LIMA, S. L. 2002. Putting predators back into behavioral predator–prey interactions. *Trends Ecol. Evol.* **17**: 70–75.
- MANN, J., S. OTT, H. L. PÉCSÉLI, AND J. TRULSEN. 2006. Laboratory studies of predator–prey encounters in turbulent environments: Effects of changes in orientation and field of view. *J. Plankton Res.* **28**: 509–522.
- PAFFENHÖFER, G.-A., J. R. STRICKLER, K. D. LEWIS, AND S. RICHMAN. 1996. Motion behavior of nauplii and early copepodid stages of marine planktonic copepods. *J. Plankton Res.* **18**: 1699–1715.
- PURCELL, J. E., AND M. B. DECKER. 2005. Effects of climate on relative predation by scyphomedusae and ctenophores on copepods in Chesapeake Bay during 1987–2000. *Limnol. Oceanogr.* **50**: 376–387.
- ROTHSCHILD, B. J., AND T. R. OSBORN. 1988. Small-scale turbulence and plankton contact rates. *J. Plankton Res.* **10**: 465–474.
- SHAHEEN, P. A., L. L. STEHLIK, C. J. MEISE, A. W. STONER, J. P. MANDERSON, AND D. L. ADAMS. 2001. Feeding behavior of newly settled winter flounder (*Pseudopleuronectes americanus*) on calanoid copepods. *J. Exp. Mar. Biol. Ecol.* **257**: 37–51.
- SHEPHERD, T. D., K. E. COSTAIN, AND M. K. LITVAK. 2000. Effect of development rate on the swimming, escape responses and morphology of yolk-sac stage larval American plaice, *Hippoglossoides platessoides*. *Mar. Biol.* **137**: 737–745.
- SIEGEL, S. 1956. *Nonparametric statistics for the behavioral sciences*. McGraw-Hill.
- SIH, A., G. ENGLUND, AND D. WOOSTER. 1998. Emergent impacts of multiple predators on prey. *Trends Ecol. Evol.* **13**: 350–355.
- STRICKLER, J. R. 1975. Swimming of planktonic *Cyclops* species (Copepoda, Crustacea): Pattern, movements and their control, p. 599–613. *In* T. Y.-T. Wu, C. J. Brokaw and C. Brennan [eds.], *Swimming and flying in nature*. V. 2. Plenum.
- SUCHMAN, C. L., AND B. K. SULLIVAN. 1998. Vulnerability of the copepod *Acartia tonsa* to predation by the scyphomedusa *Chrysaora quinquecirrha*: Effect of prey size and behavior. *Mar. Biol.* **132**: 237–245.
- SULLIVAN, B. K., C. L. SUCHMAN, AND J. H. COSTELLO. 1997. Mechanics of prey selection by ephyrae of the scyphomedusa *Aurelia aurita*. *Mar. Biol.* **130**: 213–222.
- SVETLICHNYI, L. S. 1987. Speed, force and energy expenditure in the movement of copepods. *Oceanology* **27**: 497–502.
- TISELIUS, P., AND P. R. JONSSON. 1990. Foraging behavior of six calanoid copepods: Observations and hydrodynamic analysis. *Mar. Ecol. Prog. Ser.* **66**: 23–33.
- TITELMAN, J., AND T. KIØRBOE. 2003. Predator avoidance by nauplii. *Mar. Ecol. Prog. Ser.* **247**: 137–149.
- TRAGER, G., Y. ACHITUV, AND A. GENIN. 1994. Effects of prey escape ability, flow speed, and predator feeding mode on zooplankton capture by barnacles. *Mar. Biol.* **120**: 251–259.
- VIITASALO, M., T. KIØRBOE, J. FLINKMAN, L. W. PEDERSEN, AND A. W. VISSER. 1998. Predation vulnerability of planktonic copepods: Consequences of predator foraging strategies and prey sensory abilities. *Mar. Ecol. Prog. Ser.* **175**: 129–142.
- WAGGETT, R. J. 2005. Ecological, biomechanical and neurological correlates of escape behavior in calanoid copepods. Ph.D. thesis, Univ. Texas at Austin.
- , AND E. J. BUSKEY. 2006. Copepod sensitivity to flow fields: Detection by copepods of predatory ctenophores. *Mar. Ecol. Prog. Ser.* **323**: 205–211.
- , AND ———. 2007. Calanoid copepod escape behavior in response to a visual predator. *Mar. Biol.* **150**: 599–607.
- , AND J. H. COSTELLO. 1999. Capture mechanisms used by the lobate ctenophore, *Mnemiopsis leidyi*, preying on the copepod *Acartia tonsa*. *J. Plank. Res.* **21**: 2037–2052.
- WEATHERBY, T. M., AND P. H. LENZ. 2000. Mechanoreceptors in calanoid copepods: Designed for high sensitivity. *Arthropod Struct. Dev.* **29**: 275–288.
- WIGGERT, J. D., A. G. E. HASKELL, G.-A. PAFFENHÖFER, E. E. HOFMANN, AND J. M. KLINCK. 2005. The role of feeding behavior in sustaining copepod populations in the tropical ocean. *J. Plankton Res.* **27**: 1013–1031.
- WILLIAMS, P. J., J. A. BROWN, V. GOTCEITAS, AND P. PEPIN. 1996. Developmental changes in escape performance of five species of marine larval fish. *Can. J. Fish. Aquat. Sci.* **53**: 1246–1253.
- YEN, J., AND D. M. FIELDS. 1992. Escape responses of *Acartia hudsonica* (Copepoda) nauplii from the flow field of *Temora longicornis* (Copepoda). *Ergeb. Limnol.* **36**: 123–134.

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