

# Copepod sensitivity to flow fields: detection by copepods of predatory ctenophores

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**ABSTRACT:** Copepods have the mechanoreceptive abilities to detect velocity gradients generated by approaching predators and the ability to respond to these predators within milliseconds. Ctenophores produce a low-velocity feeding current to entrain slow-swimming and non-motile prey. Since copepod species vary in their sensitivity to hydrodynamic disturbances, it is possible that species will differ in their ability to distinguish flow-generating ctenophores from the surrounding fluid. Predator-prey interactions were recorded between the ctenophore *Mnemiopsis leidyi* and 3 copepod species, *Acartia tonsa*, *Paracalanus parvus* and *Temora turbinata*. Although *A. tonsa* is more sensitive to hydrodynamic disturbances, *T. turbinata* was most successful in escaping the ctenophore predator. *T. turbinata* entered the inner lobe area (capture surfaces) of the ctenophore significantly less than either *A. tonsa* or *P. parvus* and were better able to escape both encounters and contacts with the inner lobes. These results suggest that sensitivity to velocity gradients may play only a minor role in determining escape success and an intermittent swimming pattern may increase susceptibility to capture by flow-generating predators.

**KEY WORDS:** Mechanoreception · Predator–prey interactions · Ctenophore · Escape behavior

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## INTRODUCTION

Ctenophores *Mnemiopsis leidyi* A. Agassiz (1865) are common and important predators in planktonic communities. Their ability to rapidly capture and ingest prey (Bishop 1967, Waggett & Costello 1999) and their high growth (Reeve & Walter 1978) and reproductive rates (Baker & Reeve 1974) allow them to significantly alter plankton dynamics. Their impact on planktonic communities has been documented in estuaries along the US Atlantic coast where they occur naturally (Burrell & Van Engel 1976, Deason 1982) and in the Black Sea and the Sea of Azov where they have been introduced (Shiganova et al. 2001).

Lobate ctenophores, such as *Mnemiopsis leidyi*, forage by swimming forward with their lobes spread open (Main 1928, Matsumoto & Hamner 1988). They are propelled by the beating of their 8 exterior ctene rows (Matsumoto & Hamner 1988). Continuous beating of

interior, auricular cilia creates a low velocity inward flow field, which slowly draws water into the oral lobe area (Matsumoto & Hamner 1988, Costello & Coverdale 1998).

Ctenophores are ambush-entangling predators (Greene 1985) that possess specialized capture surfaces such as tentacles or tentilla, and colloblasts (mucus-producing cells) (Franc 1978, Carré & Carré 1993, Waggett & Costello 1999). The ctenophore *Mnemiopsis leidyi* employs 2 mechanisms for capturing prey: (1) auricular cilia generate an inward flow field to capture zooplankton that have little to no motility and (2) highly motile zooplankton, such as copepods, swim directly into the capture surfaces, primarily the inner oral lobe area, where they adhere to the sticky surface (Waggett & Costello 1999). The flow field produced by the auricular cilia may also induce escape reactions in motile prey that enter the oral lobe area, either through direct swimming or entrainment in the flow field

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(Hamner et al. 1987, Matsumoto & Harbison 1993). The flow field frequently startles the prey into the capture surfaces of the ctenophore, specifically the inner oral lobes and the tentillae (Hamner et al. 1987, Matsumoto & Harbison 1993).

Copepods react to small-scale hydrodynamic disturbances in the surrounding fluid (Yen et al. 1992, Kiørboe et al. 1999), which may affect their susceptibility to predation by flow-generating predators, specifically the ctenophore *Mnemiopsis leidyi*. Although adult copepods possess the capacity to detect and avoid moving and even inanimate objects in the water column, certain copepods are unable to avoid predation by ctenophores (Bishop 1967, Waggett & Costello 1999). Since copepod species have varying degrees of sensitivity to hydrodynamic disturbances (Fields & Yen 1997, Kiørboe et al. 1999), it is possible that ctenophores are hydromechanically invisible to those copepod species with lower sensitivity.

The present study examines the hypothesis that in avoiding capture by flow-generating predators, copepods with greater sensitivity to hydrodynamic disturbances would have greater escape success from the flow-generating predator, *Mnemiopsis leidyi*. Three similarly sized, estuarine copepod species, *Acartia tonsa*, *Paracalanus parvus* and *Temora turbinata*, were exposed to the ctenophore *M. leidyi* and predator–prey interactions were observed. The sensitivity of *A. tonsa* has been examined by a number of researchers. In response to a siphon flow, the threshold shear value of adult *A. tonsa* has been reported to be  $<0.6 \text{ s}^{-1}$  (Fields & Yen 1997 [adjusted by Kiørboe et al. 1999], Kiørboe et al. 1999, Waggett & Buskey 2006a). Recently, threshold sensitivities of 4.25 and  $2.71 \text{ s}^{-1}$  were obtained for *P. parvus* and *T. turbinata*, respectively (Waggett & Buskey 2006a). Given this information, we would therefore expect *A. tonsa* to have the greatest escape success during interactions with *M. leidyi*, with *T. turbinata* escaping slightly more often than *P. parvus*.

## MATERIALS AND METHODS

**Animal collection and care.** *Mnemiopsis leidyi* were collected by hand-dipping with a plastic beaker from the surface waters of the marina at The University of Texas Marine Science Institute, Port Aransas, Texas, USA ( $27^{\circ} 50.3' \text{ N}$ ;  $97^{\circ} 03.1' \text{ W}$ ). They were maintained in 8.3 l aquaria into which continuously-flowing filtered seawater from the Aransas Ship Channel was pumped slowly. Ctenophores were fed 1 to 2 times daily with newly hatched *Artemia salina* nauplii, and their diet was supplemented 2 to 3 times a week with wild zooplankton.

We chose 3 calanoid species of similar size and various routine swimming behaviors (see below), *Acartia tonsa*,

*Paracalanus parvus*, and *Temora turbinata*, to evaluate the ability of copepods to detect flow-generating predators. Copepods were collected by tying a 0.5 m diameter 153  $\mu\text{m}$  mesh plankton net to The Marine Science Institute pier and allowing it to stream in the Aransas Ship Channel for approximately 10 min, depending on the velocity of the current. Contents of the cod end were placed in a small plastic bucket and diluted with seawater prior to returning to the laboratory. Plankton samples were gently scooped from the bucket using a plastic ladle and were examined under a dissecting microscope. Adults of the 3 calanoid species were isolated using a wide-bore pipette into 50 ml plastic beakers containing 0.2  $\mu\text{m}$  porosity filtered seawater. Copepods were used for experimentation within 1 h of sorting.

**Copepod swimming patterns.** For each copepod, 8 groups of 5 individuals were isolated. A single group was then added to a  $2.3 \times 8.0 \times 4.0 \text{ cm}$  clear acrylic plastic chamber filled with 0.2  $\mu\text{m}$  porosity filtered seawater. They were given a 10 min acclimation period. Routine swimming behavior of the copepod species was then recorded for 2 min with standard videographic techniques using a video camera (Cohu model 3315) equipped with a Nikon Nikkor 55 mm lens. The chamber was backlit using a ring of near-infrared light emitting diodes. Experiments were repeated for the remaining copepod groups (24 groups in all). Swimming behavior was analyzed to determine both routine swimming speeds and patterns.

**Predator–prey interactions.** We ran 5 sets of experiments for each copepod species. In each experiment approximately 100 copepods were used along with a different individual ctenophore predator ca. 2 cm in total length. Interactions were recorded ( $30 \text{ frames s}^{-1}$ ) for 30 min using a camera (Cohu, model 3315) equipped with a Nikon Nikkor 55 mm lens.

**Details of copepod escape reactions were examined by recording predator–prey interactions.** A small ctenophore ( $<2 \text{ cm}$ ) was placed within a narrow  $9.1 \times 5.0 \times 9.7 \text{ cm}$  clear acrylic plastic chamber filled with 0.2  $\mu\text{m}$  filtered seawater. The ctenophore was held stationary by tethering it to a 20  $\mu\text{l}$  borosilicate capillary pipette, using the method described by Waggett & Costello (1999). The pipette was attached to the aboral end of the ctenophore by applying slight vacuum pressure, and was held in place by a small clamp. After a 10 min acclimation period, approximately 100 copepods of a single species were added to the chamber. Escape reactions were recorded at  $1000 \text{ frames s}^{-1}$  using a Redlake MotionMeter<sup>®</sup> model 1130-0003 and played back at  $30 \text{ frames s}^{-1}$  for recording on standard video using a Panasonic AG1960 videocassette recorder. Experiments were replicated 6 times for *Acartia tonsa* and *Paracalanus parvus*, and 8 times for *Temora turbinata*, in order to observe approximately

50 escape reactions per species. Illumination was provided by a fiberoptic light centered on the ctenophore and a ring of infrared light-emitting diodes to increase light for imaging and to compensate for the shortened exposure time of the high-speed camera. A ruler was videotaped at the end of each experiment for calibrating distances. Video-computer motion analysis techniques were used to determine escape speed, acceleration, and number of thrusts per jump for each species (Buskey et al. 2002).

**Video analysis.** Interactions between the ctenophore and the copepods were reviewed via slow-motion playback. Frame-by-frame analysis allowed quantification of the events. Events in the interaction were categorized using the terminology and criteria defined by Waggett & Costello (1999) (Table 1). These criteria were adapted from the predation model first described by Holling (1959). Interactions between a copepod and ctenophore are interpreted as a chronological sequence in which the copepod may exhibit an escape reaction upon encountering the ctenophore or it may require direct contact with the ctenophore to initiate the reaction (Table 1).

The high-speed video recordings of individual copepods jumping to escape from the ctenophore were analyzed to evaluate the kinetics of each species' escape reactions. Components measured included speed, acceleration, and the number of pereopod thrusts per escape reaction. Individual escape jumps were played through the Motion Analysis VP-110 video-to-digital processor and digitized images were then processed using the ExpertVision Cell-Trak system. Swimming path, speed, acceleration, and number of thrusts per jump were calculated for each of the observed escape reactions.

**Statistical analysis.** Statistical analyses were performed with Systat software (v11). Results of predation events were compared using 1-way analysis of variance (ANOVA) with pairwise multiple comparisons using the Tukey HSD (honestly significantly different) test. High-speed kinetics of the 3 species' escape reactions were compared with a Kruskal-Wallis 1-way ANOVA with pairwise multiple comparisons using Dunn's Method.

## RESULTS

### Copepod swimming patterns

Swimming patterns differed among the 3 copepod species. However, no significant differences were found in the mean swimming speeds of *Acartia tonsa*,  $1.42 \pm 0.18 \text{ mm s}^{-1}$  (mean  $\pm$  SD), *Paracalanus parvus*,  $1.83 \pm 0.47 \text{ mm s}^{-1}$  and *Temora turbinata*,  $1.81 \pm 0.55 \text{ mm s}^{-1}$ . *A. tonsa* and *P. parvus* both displayed a typical 'hop-and-sink' swimming pattern (Fig. 1A,B); however, *A. tonsa* exhibited more frequent 'hops' and reached greater speeds during these hops than *P. parvus* (Fig. 1A,B). *T. turbinata* was a continuous cruiser, maintaining a more constant forward swimming pattern (Fig. 1C).

### Predator-prey interactions

Despite the abilities of the copepods to perceive artificially produced flow fields, all 3 species frequently encountered the ctenophore predator, *Mnemiopsis leidyi*, determined either by the direct contact of the copepod with the ctenophore or by the detection and escape response of the copepod. All species had a similar rate of encounters over time with the ctenophore; however, there were significant differences between the species in the frequency of encounters with the inner (Fig. 2, ANOVA,  $p < 0.0005$ ) and outer surfaces of the ctenophore (ANOVA,  $p < 0.0005$ ). *Temora turbinata* had significantly more encounters with the outer surfaces of the ctenophore than either *Acartia tonsa* (Fig. 2, Tukey HSD,  $p < 0.001$ ) or *Paracalanus parvus* (Tukey HSD,  $p < 0.0005$ ) and less encounters with the inner surfaces.

The number of escape reactions over time from the ctenophore also differed significantly among the 3 copepod species (ANOVA,  $p = 0.002$ ). *Temora turbinata* displayed significantly more escape reactions than *Acartia tonsa* (Tukey HSD,  $p = 0.0005$ ). The majority of *T. turbinata*'s escape reactions were in response to the outer ctenophore surfaces whereas *Paracalanus parvus* had significantly more escape reactions

Table 1. Terminology used for classification of predation events between copepods and a ctenophore predator, *Mnemiopsis leidyi* (modified after Waggett & Costello 1999)

Behavior	Criteria
Encounter	Initiated either by direct contact, lobe response by the ctenophore, or copepod escape reaction
Contact	Contact between a copepod and ctenophore or capture of a copepod by the ctenophore
Escape reaction	Rapid locomotor response by a copepod propelling the copepod forward at a high speed
Escape	Copepod avoids ensnarement and consumption
Capture	Copepod is consumed by the ctenophore

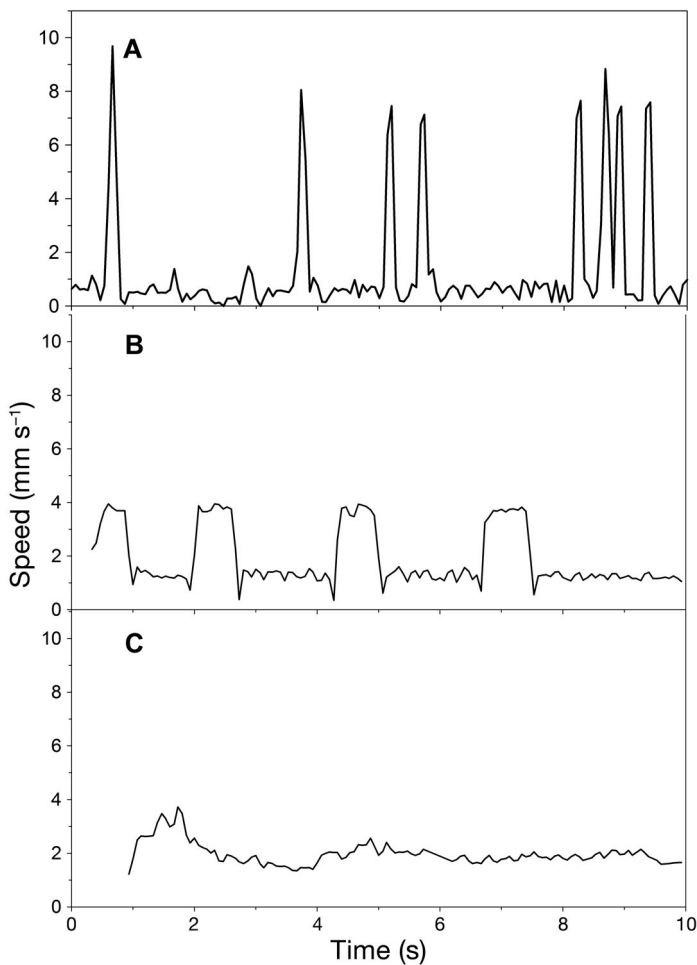


Fig. 1. Examples of routine swimming speed patterns for the 3 copepod species (A) *Acartia tonsa*, (B) *Paracalanus parvus*, and (C) *Temora turbinata*. Each path is based on the swimming path of a single copepod during a 10 s period

to the inner surfaces of the ctenophore than either *A. tonsa* or *T. turbinata* (Tukey HSD,  $p = 0.01$  and  $p < 0.0005$ , respectively).

*Paracalanus parvus* had statistically more direct contacts with the ctenophore than either *Acartia tonsa* or *Temora turbinata* (Tukey HSD,  $p = 0.048$  and  $p = 0.037$ ). There were significant differences among species in the number of contacts with the inner surfaces of the ctenophore (ANOVA,  $p < 0.0005$ ). *P. parvus* contacted the inner lobe surfaces with the greatest frequency and *T. turbinata* with the least (Tukey HSD multiple comparisons).

Significant differences were found among the rate of captures of the 3 copepod species (Fig. 3, ANOVA,  $p < 0.0005$ ). *Paracalanus parvus* was captured significantly more often than *Acartia tonsa* or *Temora turbinata* (Fig. 3, Tukey HSD,  $p = 0.002$  and  $p = 0.000$ , respectively). *T. turbinata* was captured significantly less often than *A. tonsa* (Tukey HSD,  $p = 0.003$ ).

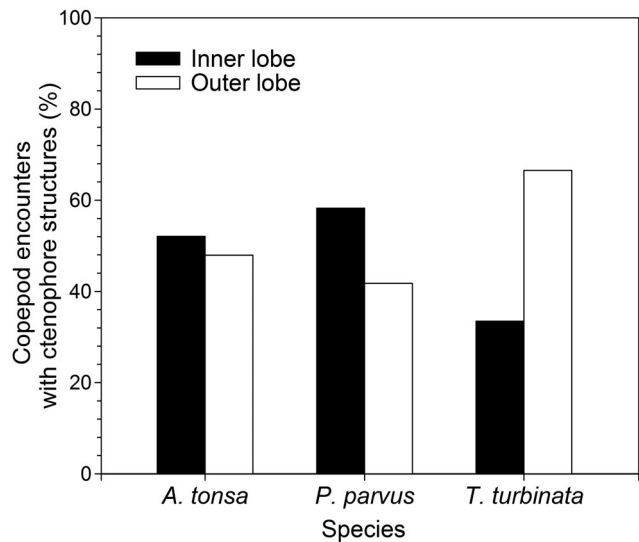


Fig. 2. *Acartia tonsa*, *Paracalanus parvus* and *Temora turbinata*. Percentage of copepod encounters with the inner and outer surfaces of the oral lobes of *Mnemiopsis leidyi*

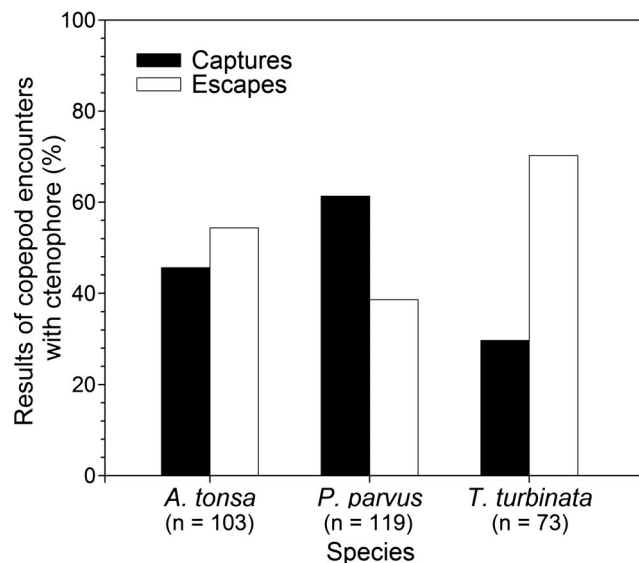


Fig. 3. *Acartia tonsa*, *Paracalanus parvus* and *Temora turbinata*. Percentage of encounters with the inner oral lobe surface of *Mnemiopsis leidyi* that resulted in copepod capture or escape

Escape performance from the ctenophore also varied among copepod species. *Paracalanus parvus* had the fastest average (Fig. 4,  $207.7 \text{ mm s}^{-1}$ ) and maximum (Fig. 5,  $413.4 \text{ mm s}^{-1}$ ) escape speeds (Kruskal-Wallis ANOVA on Ranks,  $p \leq 0.0005$ ). These speeds were significantly faster than those reached by *Temora turbinata* (Dunn's method,  $p < 0.05$ ). *P. parvus* also displayed significantly faster maximum accelerations than either *Acartia tonsa* or *T. turbinata* (Fig. 6, Kruskal-Wallis ANOVA,  $p \leq 0.0005$ , Dunn's method,  $p < 0.05$ ).

## DISCUSSION

Of the 3 copepod species examined, *Temora turbinata* was best able to avoid contact with the inner surfaces of the ctenophore. The surface area of the outer and inner lobes of a ctenophore ca. 1.5 cm long would be 3.6 cm<sup>2</sup> and 0.98 cm<sup>2</sup>, respectively. If copepod encounters were proportional to the surface area of the ctenophore, we would expect significantly more encounters with the outer lobes. This was observed only by *T. turbinata*, suggesting that either *Acartia tonsa* and *Paracalanus parvus* were actively avoiding the outer lobes, or they were more frequently entrained by the ctenophore's flow field. This finding is interesting, since *A. tonsa* is known to have a lower threshold deformation rate (0.57 s<sup>-1</sup>, Waggett & Buskey 2006a, 0.34 s<sup>-1</sup> Fields & Yen 1997 [adjusted by Kiørboe et al. 1999], 0.38 s<sup>-1</sup>, Kiørboe et al. 1999), i.e. greater sensitivity to hydrodynamic disturbances, than either *T. turbinata* (2.71 s<sup>-1</sup>, Waggett & Buskey 2006a) or its congener *T. longicornis*, (6.50 s<sup>-1</sup>, Kiørboe et al. 1999). *T. turbinata* was better able to escape an encounter with the ctenophore once it contacted the sticky inner surfaces of the ctenophore.

Several factors may contribute to the escape success of *Temora turbinata*. First, its morphology may reduce the number of captures. Copepods are most vulnerable to capture when their pereopods become entangled in the mucus coating on the inner oral lobe surfaces of the ctenophore (Costello et al. 1999). The rounded dorsal exoskeleton provides the largest surface area on *T. turbinata* and contributes to a disproportionately large percentage of its total body surface area, compared to other copepod species. This large dorsal surface area, and the contributing body proportions, may reduce the chance of a contact with the vulnerable pereopods. Furthermore, *T. turbinata* has shorter antennal setae, suggesting that they too are less susceptible to entanglement. Routine swimming patterns of the 3 copepod species also varied, and *T. turbinata* was the only continuous cruiser observed. We speculate that the intermittent swimming pattern displayed by *Paracalanus parvus* and *Acartia tonsa* may allow them to become entrained in the ctenophore flow field and brought into the inner lobe area more frequently. Although *A. tonsa* has a lower average shear threshold than *T. turbinata*, their sensitivity would differ during the 'hops' and 'sinks' of their 'hop-and-sink' swimming. During 'hops', *A. tonsa* swims at a mean speed of 5.7 mm s<sup>-1</sup>. At this speed, *A. tonsa* would be capable of detecting shear greater than 22.5 s<sup>-1</sup> (calculated from Visser 2001) a value much higher than the threshold of *T. turbinata* (2.71 s<sup>-1</sup>).

Copepods are also capable of modifying their behavior relative to the type and strength of the associated

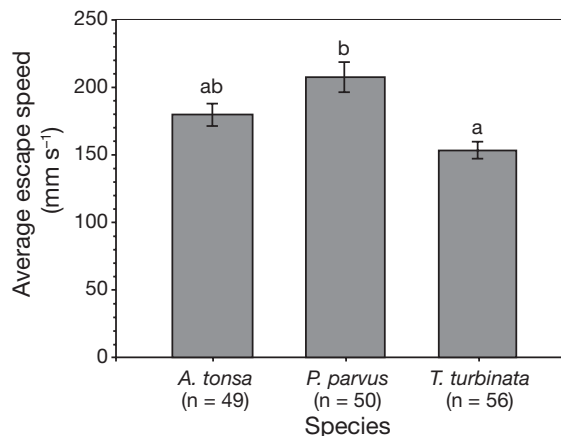


Fig. 4. *Acartia tonsa*, *Paracalanus parvus* and *Temora turbinata*. Average speed achieved by copepods during escapes from *Mnemiopsis leidyi*. Speeds of species that share the same letter (a,b) are not significantly different (Kruskal-Wallis 1-way ANOVA,  $p < 0.05$ )

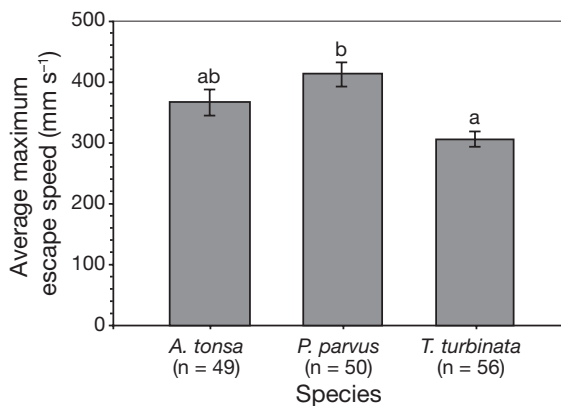


Fig. 5. *Acartia tonsa*, *Paracalanus parvus* and *Temora turbinata*. Average maximum speeds achieved by copepods during escapes from *Mnemiopsis leidyi*. Speeds of species that share the same letter (a,b) are not significantly different (Kruskal-Wallis 1-way ANOVA,  $p < 0.05$ )

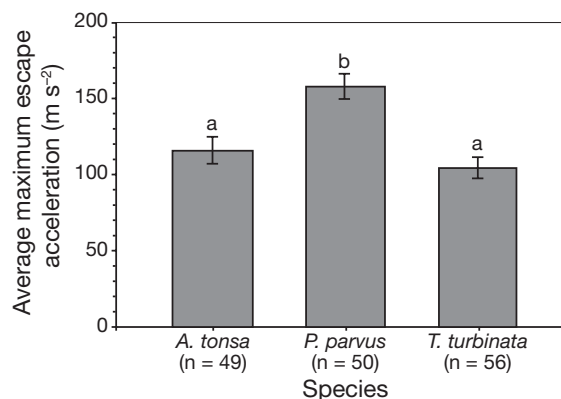


Fig. 6. *Acartia tonsa*, *Paracalanus parvus* and *Temora turbinata*. Average maximum accelerations achieved by copepods during escapes from *Mnemiopsis leidyi*. Accelerations of species that share the same letter (a,b) are not significantly different (Kruskal-Wallis 1-way ANOVA,  $p < 0.05$ )



stimulus. Kinetic performance of *Paracalanus parvus* and *Temora turbinata* has been evaluated in response to an attacking fish, the hemisessile blenny *Acantheblemaria spinosa*, and all 3 species were exposed to a repeatable near-field hydrodynamic stimulus (Waggett 2005). *T. turbinata* responded with greater maximum and average speeds and maximum accelerations in response to the blenny compared to the near-field hydrodynamic stimulus. *P. parvus* had similar escape speeds to both the blenny and the ctenophore; however, accelerations were much greater in response to the ctenophore. The near-field hydrodynamic stimulus elicited much weaker escape responses in all 3 species in comparison to the blenny and ctenophore results. Copepod escape behavior indicates that the blenny and the ctenophore predators created stronger hydrodynamic stimuli and were perceived as a greater threat to survival than the near-field hydrodynamic stimulus (Waggett 2005).

Copepod escape success from the ctenophore, *Mnemiopsis leidyi*, is a function of swimming behavior, body structure, and orientation at the time of contact. Their sensitivity to water movements may play only a minor role in their ability to successfully avoid capture by ambush-entangling predators such as the ctenophore, *M. leidyi*. Copepods are also highly susceptible to predation by visual predators and were captured almost 80% of the times they were attacked by *Acantheblemaria spinosa* (Waggett & Buskey 2006b). Although *Paracalanus parvus* has a significantly faster response latency and displays an intermittent swimming pattern, they were still captured frequently by the blenny, indicating these behavioral components did not enhance their escape success. A similar result was found in the predator–prey interactions with *M. leidyi*. *Temora turbinata* escaped significantly more often than either *P. parvus* or the more sensitive (lower shear threshold), *Acartia tonsa*. Copepod escape success is therefore a complex process, resulting from the integration of various components (i.e. kinetics, response latency, shear threshold etc.), which are difficult to predict, considering the copepod's ability to modify its behavior and the predator's ability to adjust their attack behavior.

Despite their abilities to detect minute fluid disturbances on the scale of nanometers (Yen et al. 1992, Buskey et al. 2002), copepods are still preyed upon and consumed by flow-generating predators, such as ctenophores, at high rates. Ctenophores have been estimated to crop as much as 31% of zooplankton population density daily (Bishop 1967, Deason 1982). The water disturbances created by the ctenophore appear to be below the threshold for detection by many copepod species. As ambush-entangling predators, ctenophores rely on flow-generating mechanisms and the

movement of their prey to initiate encounters. Ctenophores swim slowly through the water column at rates of 0.6 cm s<sup>-1</sup> while foraging for prey (Matsumoto & Harbison 1993, Kreps et al. 1997). The low velocity flow field created by the constant beating of their auricular cilia may act to reduce the production of the forward bow wave made by the forward swimming ctenophore.

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