

## Can Copepods Differentiate Prey from Predator Hydromechanically?

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**Jiang-Shiou Hwang and Rudi Strickler (2001)** Can copepods differentiate prey from predator hydro-mechanically? *Zoological Studies* 40(1): 1-6. Copepods use hydromechanical signals to detect prey and predators. However, little is known about their ability to differentiate prey from predators, neither from random water flow. We used laser- and video-optical equipment with a modified Schlieren optical pathway to observe a tethered copepod under variable hydrodynamic conditions. The results suggest that the copepod can distinguish between hydromechanical signals generated by an external source and those created by its own feeding current, even when these disturbances are within a similar speed range, as defined by measurements of spatial displacement of suspended particles. The data suggests that planktonic copepods may use a simple form of pattern recognition to distinguish between sources of signals: predators, prey, or random flow.

**Key words:** Calanoids, *Centropages hamatus*, Random flow, Escape reactions, Pattern recognition.

Copepods are sensitive to hydromechanical disturbances (e.g., Schröder 1967, Strickler and Bal 1973, Strickler 1975a, Costello et al. 1990, Marrase et al. 1990, Hwang 1991, Hwang et al. 1994, Wong 1995, Kjørboe et al. 1999). Mechanoreceptors on the antennules (1st antennae) of copepods are responsible for reception (e.g., Strickler and Bal 1973, Huys and Boxshall 1991, Yen et al. 1992, Lenz and Yen 1993). They detect both prey (e.g., Landry 1980, Legier-Visser et al. 1986) and simulated predators (Strickler 1975a, Wong 1980). Hydromechanical signals are considered the most important factor in predator-prey interactions of copepods (e.g., Strickler and Bal 1973, Kerfoot 1978, Zaret 1980). Little is known, however, about the underlying principles governing the ability of copepods to hydro-mechanically differentiate between predators, prey, and random water flow (also see Yen and Strickler 1996). To explore this question, we created an artificial and random hydromechanical signal. We then exposed a tethered copepod to periodic random flow simulating the variable hydromechanical cues occurring in nature (Hwang 1991, Hwang and Strickler 1994, Hwang et al. 1994).

Planktonic copepods are primary grazers of phytoplankton and a food source for planktivorous fish, and, therefore, key elements in the human food supply. It is of importance to figure out whether copepods rely solely on hydromechanical signals to differentiate prey from predators or whether other information, such as chemicals (Dzyuban 1937 1939, Fryer 1957, Kerfoot 1978), are needed. If chemicals are important messengers, then man-made chemical pollution may disrupt a major link in the aquatic and marine food web.

### MATERIALS AND METHODS

The data used here are a subset of data derived from a large set of experiments concerning the interactions between planktonic copepods and random flow (Hwang 1991). The materials and methods used to capture, maintain, tether, and videotape a copepod, *Centropages hamatus*, are described in Hwang (1991), Hwang et al. (1993), Hwang et al. (1994), and Hwang and Strickler (1994). Note that in these and other earlier reports we talked about "tur-

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bulence" when addressing random flow. Fluid-dynamicists have made us aware of the fact that we were not generating the full scales of turbulence and, therefore, should not use this well-defined expression.

The experiment was conducted in a dark room at 18 °C. The laser- and video-optical system is described in Strickler and Hwang (1999). An infrared-sensitive camera (Panasonic WV-1800) and a video-cassette recorder (Panasonic NV-8500) were used for video recording. Each frame was time marked sequentially by a QSI frame counter. The temporal resolution, as determined by the video frame rate, was 1/30 s. The spatial resolution was 5  $\mu\text{m}$ . An editing controller (Panasonic NV-A500) facilitated frame-by-frame videotape analysis.

An aluminum mesh attached to a motor from an electric toothbrush provided the vibration necessary to produce random flow in the experimental vessel (Costello et al. 1990). A vessel containing 5 L of 0.22  $\mu\text{m}$  filtered seawater and 100 cells/ml of *Thalassiosira weissflogii* cells provided the experimental environment.

### Experimental design

The experiment began with a 25-min calm-water period during which no hydromechanical stimuli were introduced into the experimental vessel. The only water movement was the result of the on-and-off feeding current created by the tethered copepod itself. This was followed by a 25-min period of artificial agitation utilizing the described apparatus. This alternation between calm and random flow periods was replicated 4 times at 25-min intervals (Fig. 1). Even though no induced random flow occurred during the calm periods, residual effects from the previous periods kept the water in motion and decayed over about 7 min, after which time the water was visually calm.

The 4 cycles of 25-min calm and agitated periods, were followed by 3 cycles with 12.5-min intervals. Finally, the alternation of quiescence and random flow was replicated 3 times at 6.25-min intervals (Fig. 1). All of these experiments were conducted sequentially and continuously resulting in over  $5 \times 10^5$  recorded video frames and a database 25 MB in size.

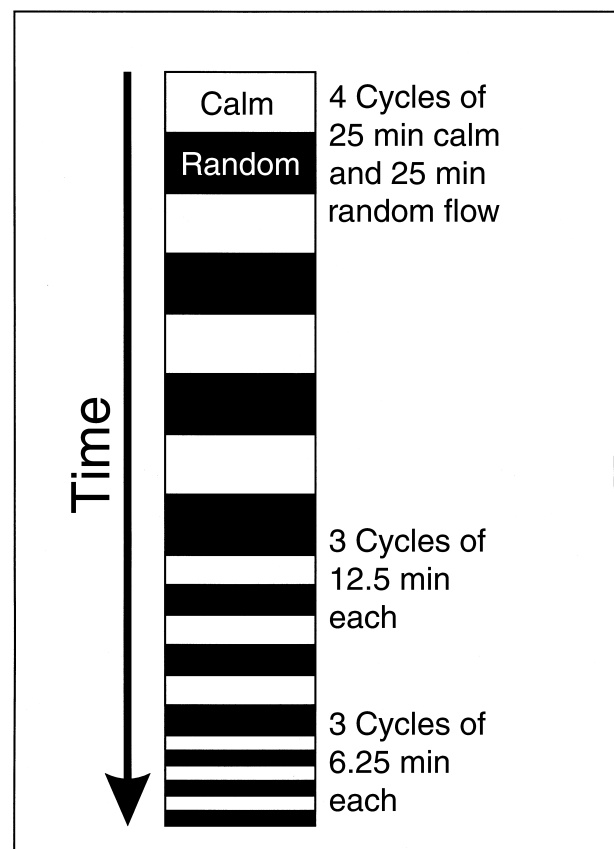
### Data analysis

The strengths of the threshold hydromechanical signals were determined by measuring particle speeds (e.g., Trager et al. 1990) at the onset of the

escape response during all periods of artificial agitation. The path lines of the particles entrained in the feeding current were tracked and their speeds were determined at a location 1 mm directly above the antennules. When an escape response was triggered, the flow field around the copepod at escape initiation was mapped and particle speeds determined. The feeding current of the copepod in calm water and the random flow fields which triggered the escape reactions of the tethered copepod were mapped using Corel Draw software.

## RESULTS

The change from calm water to random flow was critical for stimulating the escape response in the copepod. In our study, the strength of the random flow was determined by measuring particle speeds, which fluctuated between 3 and 34 mm/s during periods of induced random flow. When a hydromechanical disturbance was created which exceeded the threshold, *Centropages hamatus* imme-



**Fig. 1.** Schematic diagram of the time course of a copepod exposed to periodic hydromechanical stimuli.

diately initiated an escape response. Table 1 shows the minimum particle speeds which induced escape responses. The lowest thresholds were at speeds of 0.84 and 0.87 mm/s (1st and 4th 25-min random flow periods, respectively). Copepods were most sensitive during the 1st 25-min random flow period. The sensitivity decreased as *C. hamatus* was subjected to increased exposure to random flow stimuli (Table 1), especially, after the shortest calm periods, which were shorter than the time needed to reach truly calm water (see above).

Calanoid copepods create feeding currents to assist in gathering and detecting prey (Strickler 1982). Figure 2 shows the typical flow field of *C. hamatus* during feeding. In the videotape analysis of the flow field, only particle motions modified by the presence of a feeding current were processed. The feeding current speed was 0.79 mm/s as derived from particles starting 1 mm away from the antennules. Figure 3 shows a flow field during a random motion period. This flow field triggered an escape reaction.

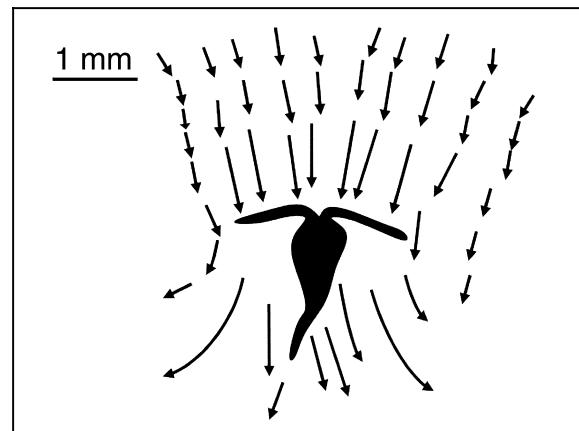
As mentioned earlier, this set of experiments has produced additional results, which have been published elsewhere answering different questions. In Hwang et al. (1994) we established the fact that calanoid copepods show habituation behavior. Its figure 1 shows the time course of escape reactions during the first 7 transitions from calm to random flow conditions. Its figure 2 depicts the percent of time spent by the animal in the slow-swimming mode, showing the averages and 95% confidence intervals for each period of calm water or random flow. Additional figures and calculations are dedicated to the time course of fast-swimming (escape) events.

In Hwang and Strickler (1994), all transitions from calm to random flow were included in the evaluations. Particle speeds versus temporal ranking of escape reaction were plotted in several figures. The evaluations concentrated on the question of habituation and fatigue due to continuous stimulation of escape reactions.

**DISCUSSION**

Most planktonic copepods are optically transparent in order to minimize predation from visually hunting fish (e.g., Zaret 1972, Zaret and Kerfoot 1975). To be chemically “transparent” may not be an insurmountable challenge either. Most calanoid copepods release their metabolic by-products within fecal pellets giving almost no cues as to the location of the animal. Swarming zooplankters may still leave a trail of fecal pellets leading a potential predator to the swarm. However, Isaacs, in Behrman (1992), suggested that animals in swarms should show ‘synchronicriturition’—same-time release of metabolic by-products—in order to minimize detection due to an odor trail.

The question then is how can a copepod be “transparent” in terms of mechanoreception? Small sizes, streamlined shapes, and slow and continuous movements may be ways to minimize the generation of large signals and, therefore, the probability of detection (Zaret 1980). In addition, water is always in motion and mechanoreceptors will perceive its mo-



**Fig. 2.** Dorsal view of *Centropages hamatus* when generating its own feeding current. Note the typical path of entrained particles. Each arrow shows the path line of a particle during a 1-s interval.

**Table 1.** Particle speeds triggering copepod escape responses during the switch from calm to random flow. The data include 4 replications of the 25-min periods of random flow, and 3 replications each of the 12.5- and 6.25-min periods of random flow

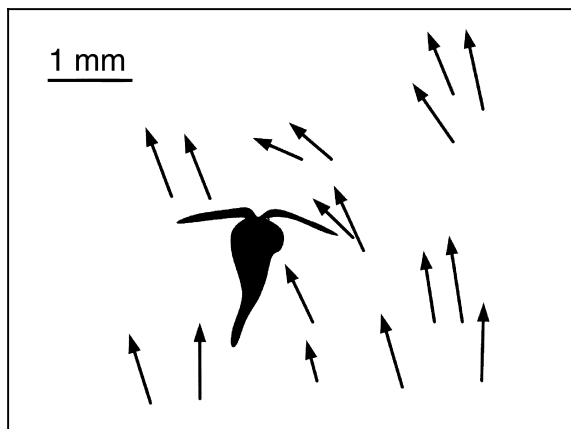
25-min random flow periods				12.5-min random flow periods			6.25-min random flow periods		
particle speed triggering escape response (mm/s)				particle speed triggering escape response (mm/s)			particle speed triggering escape response (mm/s)		
0.84	4.15	4.29	0.87	3.99	4.96	5.42	6.89	8.00	10.99

tion regardless of the source of generation. One way a prey could minimize predation would be to “hide”—fluid-dynamical camouflage—within the signals produced by ambient water flow (see also Kerfoot 1978). Since all zooplankters have predators, they all may camouflage themselves in this way. The question arises, how can a copepod still identify its prey, predators, or mates within the “jungle” of water motions?

The animals behave according to a “worst case” scenario. When stimulated beyond a threshold level, they respond with an escape reaction (e.g., Strickler 1975a). With such behavior as the basic answer to mechanical stimuli, much energy may be expended when it is not needed, or a possible mate may be lost (e.g., Strickler 1998). In Hwang et al. (1994) and Hwang and Strickler (1994), we researched the time course of the escape reactions during periodic stimulation, and found that there was habituation, i.e., the threshold increased over time (Hwang et al. 1994). This means that zooplankters may be even less able to detect signals from other animals. And, it also means that prey should seek environments with a high degree of background random water motion. However, zooplankters might also habituate only to signals generated by random flow while maintaining sensitivity to signals generated by other sources like animals.

### Escape responses during periodic random flow

*Centropages hamatus* demonstrated escape responses immediately after the creation of a hydro-mechanical signal which exceeded a threshold. Sensitivity to mechanical stimuli of *C. hamatus* was



**Fig. 3.** Dorsal view of *Centropages hamatus* subjected to random flow and milliseconds before initiating an escape reaction. Each arrow shows the path line of a particle during a 1-s interval.

highly dependent upon the duration of the quiescent period (Table 1). The exhibited thresholds for the escape response were observed to be as low as 0.84 mm/s during the 25-min intervals and as high as 10.99 mm/s during the 6.25-min intervals (Table 1).

The energy costs of escape behaviors are much higher than those during normal swimming (Marrase et al. 1990), and in copepods, they may reach a 400-fold difference (Strickler 1975b 1977, Alcaraz and Strickler 1988). Therefore, any information which suppresses the execution of an escape reaction helps save energy. This suggests that the time-dependent threshold of *C. hamatus* during the periodic random flow events could be a function of both predation risk and energy costs.

### Escape response threshold

Escape responses have been documented in the rotifer, *Keratella* spp., under conditions such as encounters with predatory rotifers, reaction to intake currents of *Daphnia*, and imitation during *Daphnia* approach (Gilbert and Kirk 1988). All of these conditions generate hydromechanical signals and provide information to the rotifer, *Keratella*, triggering an escape reaction. The threshold for triggering an escape response in the rotifers, *Keratella*, and *Asplanchna brightwelli*, are related to the speeds in their flow fields (0.35 and 0.65 mm/s, respectively) (Gilbert and Kirk 1988). Similarly, on perceiving a hydromechanical disturbance, *C. hamatus* exhibited escape responses when the minimum particle speeds, however, were 0.84 and 0.87 mm/s higher than those in the rotifers. *C. hamatus* exhibited no escape response below these thresholds.

The question arises as to whether larger zooplankters have higher thresholds because their predators are larger than those of smaller prey. This question can be expanded when we introduce the concept of the Kolmogorov scale of turbulence. Smaller animals may live for most of their lives below the Kolmogorov scale and may not be subjected to random flow. They might not be able to find a fluid environment in which they can hide; hydrodynamical camouflage may not work. Larger copepods, especially ones living in near-shore and tidal environments, such as *C. hamatus*, may show a more complex behavioral repertoire due to their more complex fluid environment.

### Differential responses to predator and prey

Although particle speeds within the feeding current (0.79 mm/s) and random flow induced by the

external disturbance (0.84 mm/s) are in the same range, the flow fields and particle motions differ (Figs. 2, 3). This may allow *Centropages hamatus* to differentiate, mechanically, between an external disturbance generated by a potential predator or prey, and its own feeding current or an external energy source. A copepod can sense a particle at a range of approximately 1 mm (Strickler 1982, Koehl 1983, Price et al. 1983, Legier-Visser 1986, Jonsson and Tiselius 1990). Jonsson and Tiselius (1990) demonstrated that detection of individual ciliates by the antennules of the copepod does not require direct physical contact of the antennules.

The difference between the flow field in figure 2 and the one in figure 3 is that the one generated by random flow is dynamic in time and space. Along the antennules, the different mechanoreceptors will pick up randomly distributed signals, which change randomly over time. Any approaching animal, whether a prey or predator, will, however, create signals which increase according to the combined velocities of the animals (Zaret 1980). The temporal signals also have a spatial structure, decaying to the sides of the generating animal according to physical laws (Zaret 1980). This means that approaching zooplankters send hydromechanical signals ahead of themselves which change in time and space differently than would random flow (see also Yen and Strickler 1996). This also means that the many receptors on the antennules should act as receptor arrays.

We propose that such a signal pattern with its spatial and temporal components may be used to distinguish animals in random flow fields. This “pattern recognition”, primitive when compared to a visual one, is basically an extension of the detection mode postulated by Legier-Visser et al. (1986). It would explain why planktonic copepods still react to an approaching “predator” under random flow conditions with the same accurate behaviors as in calm waters (Wong 1995). Hydrodynamic camouflage may reduce the detection distance and, therefore, lower the capture rate, but it cannot fully eliminate the risk of being preyed upon. However, targeted research is needed to elucidate pattern recognition and its limitations in planktonic copepods.

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## 橈足類能否以流體之物理訊號區別其食餌與掠食者

黃將修<sup>1</sup> Rudi Strickler<sup>2</sup>

橈足類曾被證實利用流體的物理訊號去偵測其食餌或其捕食者，但卻甚少證據直接證實橈足類如何利用這樣的訊號去區別其食餌、捕食者與亂流。本研究利用雷射攝錄影系統以及改良的 Schlieren 光學系統，去研究顯微固定的橈足類在多變化的流體動力狀態下偵測食餌或捕食者的特性。本研究結果顯示，橈足類有能力區別流體的物理訊號是源自外界環境中產生或是其本身所製造的攝食流，尤其是這些流體的物理訊號已在相似的流速中甚難區別時，橈足類依然有能力加以區別。研究資料顯示，浮游的橈足類可能以簡單流體之模式認知為依據，來區別訊號源自掠食者、食餌或亂流。

**關鍵詞：** 哲水蚤，*Centropages hamatus*，亂流，避敵反應，模式認知。

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