

# Sensory perception, neurobiology, and behavioral adaptations for predator avoidance in planktonic copepods

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## Abstract

Copepods are important grazers on microplankton in marine food webs and are, in turn, preyed upon by a wide range of predators with diverse feeding adaptations. Although copepods have evolved numerous adaptations to help them avoid predation, their escape behavior sets them apart from many other planktonic organisms. Mechanoreception is widely used by copepods to detect hydrodynamic disturbances created by approaching predators. When these disturbances are detected, copepods respond quickly with escape jumps that can accelerate them from a stationary position to speeds of over 600 body lengths per second within a few milliseconds. Myelinated nerves may improve the escape behavior of some copepods through faster conduction of nerve impulses. The differences in response latencies between myelinate and amyelinate copepod species are greatest in larger copepod species, where nerve signals must be conducted over longer distances. Environmental variability such as turbulence may affect the ability of both prey to detect predators and predators to capture their planktonic prey. Small amounts of turbulence favor the predator, while too much turbulence reduces predation. Understanding the sensory physiology of copepods and their behavioral adaptations for avoiding predation will increase knowledge of the factors affecting the structure and function of marine pelagic food webs.

## Keywords

Zooplankton, copepods, sensory perception, escape behavior

## 1 Introduction

Copepods are among the more common and diverse planktonic metazoans in the sea (Humes, 1994; Longhurst, 1985). They are important links in marine food webs, feeding on a wide range of autotrophic and heterotrophic microplankton (and in some cases, mesoplankton) within the sea (Banse, 1995), and are preyed upon by a variety of invertebrate and vertebrate predators. Invertebrate predators on copepods include, among others, ctenophores, cnidarians, and chaetognaths. Most marine fish species feed on copepods during at least part of their life cycle (most larval and juvenile fish) and some species remain planktivores throughout their lives. The methods by which these predators capture copepod prey range from passive entanglement (e.g., cnidarians) to active raptorial capture (e.g., fish). The predators may locate them by random encounter, or detect their presence mainly through vision or by the hydrodynamic disturbances created by their motion (Greene, 1985). This article will briefly review the broad topic of copepod adaptations for predator avoidance, and then focus more

specifically on the roles of sensory perception and neurobiology in behavioral adaptations for avoidance of active raptorial predators on copepods.

Given the diversity of organisms that prey on copepods, and their wide variety of predatory adaptations, it is perhaps not surprising that copepods have evolved an impressive array of morphological, physiological, and behavioral adaptations to avoid predation (Ohman, 1988). Morphological adaptations such as spines, or chemical defenses such as distastefulness, may reduce the ingestion rate of zooplankton after they have been captured (Kerfoot, 1982; Morgan, 1989), however, even if zooplankton escape by means of a post-capture antipredator adaptation, there is a risk of injury during the attack. Some antipredator

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adaptations reduce the probability of an encounter with, or attack by, a potential predator. For example, diel vertical migration of copepods may reduce the encounter rate of copepods with visual predators such as fish, by swimming to depths during the day where light intensity is closer to or below the visual threshold of their predators (Frost, 1988; Zaret & Suffern, 1976). Visual predators selectively attack and consume larger and more conspicuous prey organisms (Brooks & Dodson, 1965; O'Brien, Slade, & Vinyard, 1976) making small size an adaptation against predation. Some copepods are nearly transparent, reducing the ability of visual predators to detect them (Greze, 1963), although some visual predators are capable of detecting UV wavelengths or polarized light patterns that may enhance their ability to detect otherwise transparent zooplankton (Johnsen, 2001; Shashar, Hanlon, & Petz, 1998). Reduced motion of copepod prey may diminish the likelihood of predatory attacks once they are encountered by predators, because motion patterns may make copepods more conspicuous and help visual predators distinguish them from similarly sized nonliving particles of detritus (Buskey, Coulter, & Strom, 1993; Kramer & McLaughlin, 2001; Zaret, 1980). In addition, some copepods can excrete bioluminescent liquids that may help them avoid capture by visual predators in reduced light environments by distracting them, temporarily blinding them, or attracting predators of the copepod's attacker (Hartline, Buskey, & Lenz, 1999; Porter & Porter, 1979).

In addition to this wide array of antipredator adaptations, calanoid copepods possess an extraordinary escape behavior that sets them apart from all other groups of zooplankton (Figure 1). The name *copepod* is derived from the Greek words *kope*, meaning oar, and *podos* meaning foot (Mauchline, 1998), suggesting that these small crustaceans possess limbs that are especially well adapted for rapid swimming. When stimulated to elicit an escape response, calanoid copepods exhibit extraordinarily rapid swimming speeds of over 600 body lengths per second (600 mm/s for a 1 mm copepod) with a rapid, synchronized thrust of their pereopods (swimming legs; Alcaraz & Strickler, 1988; Strickler, 1975). Copepods can respond to a hydrodynamic disturbance created by an approaching predator in as little as 2–3 ms, and can accelerate to these maximum escape speeds in just a few milliseconds, achieving accelerations of over 200 m/s<sup>2</sup> (Buskey, Lenz, & Hartline, 2002). Escape behaviors are energetically costly to copepods (Morris, Gust, & Torres, 1985; Strickler, 1975; Vlymen, 1970) and there is a trade-off between escaping unnecessarily and missing a real threat. Since unnecessary escape jumps would be both energetically costly and make the copepods more visually conspicuous to potential predators, copepods may become desensitized to lower strength stimuli or habituate to them

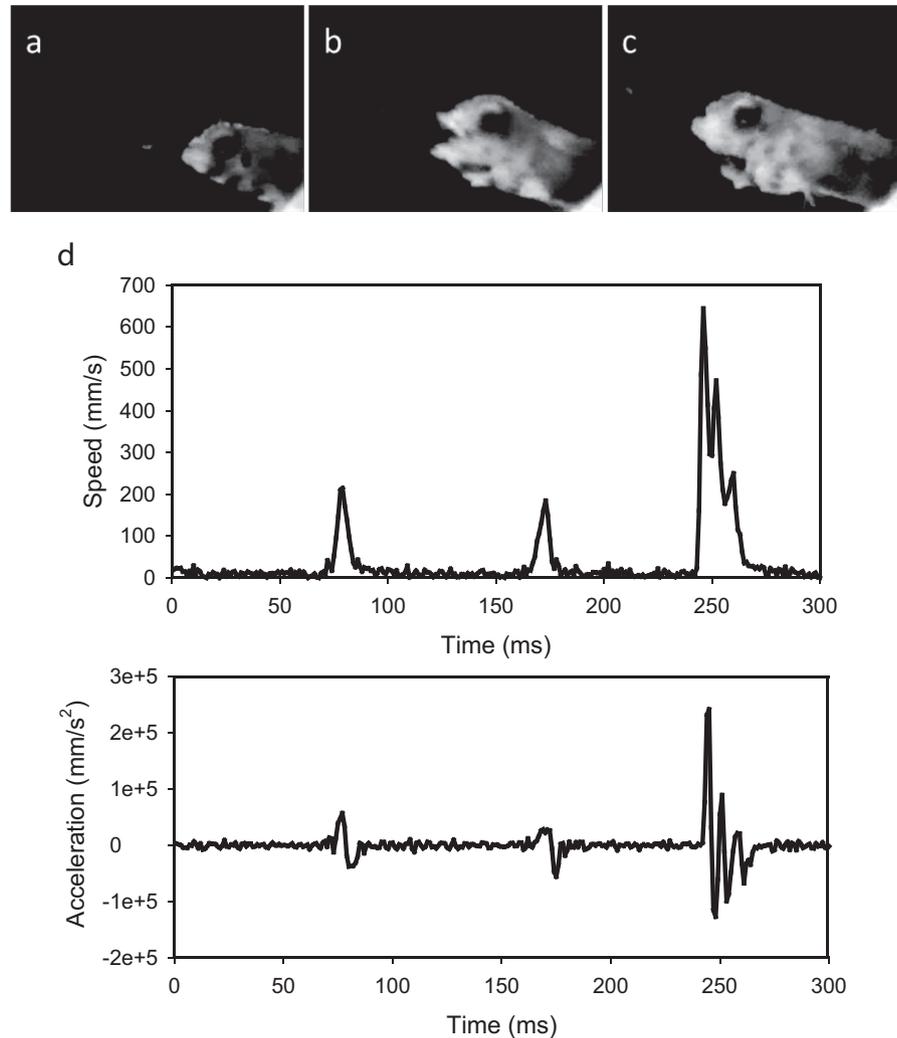
(Fields & Yen, 1997; Hwang, Costello, & Strickler, 1994).

There is a clear relationship between copepod body length and maximum swimming speed (Figure 2) that holds for different developmental stages as well as for a wide variety of calanoid copepod species. Copepod nauplii with lengths of only 0.1 mm can perform escape jumps with peak speeds approaching 600 body lengths per second (Bradley, 2009), a performance level similar to adult copepods. A similar relationship exists between body length and maximum speed for fishes (Burdick, Hartline, & Lenz, 2007; Figure 2), but the maximum speeds for copepods are approximately an order of magnitude higher for copepods compared with fish of similar length. Since many planktivorous fish are an order of magnitude longer than their prey, the maximum speeds of both predator and prey may be similar, making early detection of the approach of a predator essential to survival.

Rapid escape behavior may not be effective against all types of predators, however. Ctenophores and cnidarian medusae often use more passive prey capture methods that rely on the movement of their prey to bring them into contact with stinging cells or sticky surfaces. This group of predators can be especially voracious predators on copepods, and they can severely reduce copepod populations in some temperate coastal areas during summer (Deason & Smayda, 1982; Purcell, 1992). The overall impact of fish feeding on copepod populations is more difficult to quantify. It has been suggested that predation by planktivorous fish is not intense enough to limit copepod populations (Cushing, 1983); however, a number of antipredator adaptations that evolved in copepods are most effective against visual predators (e.g., transparency, vertical migration, bioluminescence), which argues for the ecological importance of visual, raptorial predators such as fish.

## 2 Copepod sensory systems for detecting predators

Behavioral antipredator adaptations require an understanding of the sensory systems used by copepods to detect predators. The major sensory modalities available to copepods include the abilities to detect light (photoreception), chemicals (chemoreception), and fluid motion (mechanoreception). Most copepod species possess simple naupliar eyes consisting of two dorsal ocelli and one ventral ocellus (Boxshall, 1992; Elofsson, 1966). These simple photoreceptors are not thought to be capable of image formation, but are sensitive detectors of slight changes in light intensity that are used to help regulate vertical position in the water column, and control the timing of diel vertical migration (Forward, 1976). Several species of copepods possess cuticular lenses that may allow them to obtain

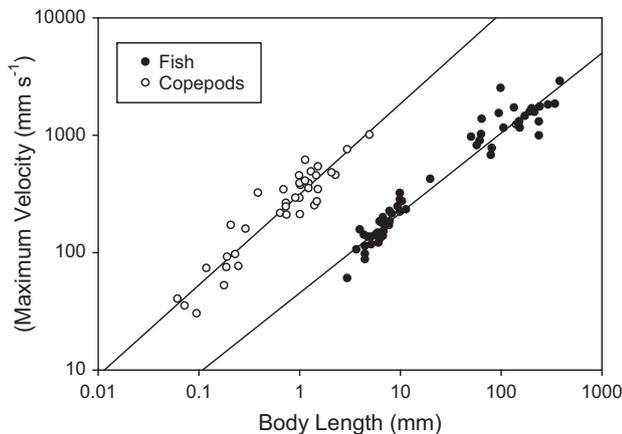


**Figure 1.** A calanoid copepod, *Acartia tonsa*, approaching a planktivorous fish, *Acanthemblemaria spinosa*, and its escape from predation. The copepod is swimming directly toward the fish's mouth at time zero (1a); 20 ms later the fish has begun its attack and the copepod has turned to perform a rapid escape jump away from the fish (1b); 37 ms later the fish completes its feeding lunge and the copepod has completed its initial escape jump (1c). Speed record from the video sequence depicted in 1a through 1c above; the peaks in speed of about 200 mm/s at approximately 80 ms and 170 ms represent normal speed repositioning jumps as the copepod approached the fish; the multiple peaks of about 650, 450, and 250 mm/s beginning at approximately 240 ms represent a high speed escape jump by the copepod (1d). Acceleration record for a same sequence, showing maximum acceleration of  $> 200 \text{ m/s}^2$  during the initial escape. Unpublished example from study of Clarke et al. (2005).

some spatial information about the distribution of light in the environment (Land, 1984). There are also reports of visual predation by copepods on other zooplankton (Gophen & Harris, 1981). Predator avoidance has not been attributed to image-forming vision in copepods.

Rapid changes in light intensity elicit escape responses in copepods, presumably as a predator avoidance mechanism. Visual systems in some copepod species have been shown to mediate a "shadow response" to rapid reductions in light intensity (Buskey & Hartline, 2003; Buskey, Mann, & Swift, 1986). Similarly, several copepod species have been demonstrated to possess a photophobic response to rapid increases in light intensity, such as those created by the stimulation of bioluminescence in a dark environment

(Buskey, Mills, & Swift, 1983; Buskey & Swift, 1985). For the limited number of species studied, different responses have been found for copepods from freshwater, estuarine, and open ocean environments (Buskey, Mann, & Swift, 1987). Four estuarine species tested all showed strong photophobic responses to flashes of light when dark adapted, as well as to rapid decreases in light when light adapted. This corresponds to the presence of both shadow-casting predators (e.g., cnidarian medusae, whose nearly transparent but curved bodies refract light and produce shadows) and bioluminescent plankton whose flashes may signal the approach of a potential predator in estuarine environments. Two species of open ocean copepods, both found primarily in the mesopelagic, showed strong



**Figure 2.** Maximum swimming velocities of fish and copepods plotted against body length. Fish data from Williams, Brown, Gotceitas, and Pepin (1996); Domenici and Blake (1997); and Shepherd, Costain, and Litvak (2000). Copepod data from Yen and Strickler (1996); Buskey et al. (2002); Lenz, Hower, and Hartline (2004); Burdick et al. (2007); Bradley, (2009); and Buskey (unpublished).

photophobic responses to light flashes in the dark, but did not respond to shadows when light adapted. This also corresponds well to the high abundance of bioluminescent plankton in the mesopelagic, while even daytime light intensities are near the visual threshold for mesopelagic copepods (Buskey, Baker, Smith, & Swift, 1989), so response to shadows may not be an important antipredator adaptation for these copepods. However, neither simulated bioluminescence nor shadows elicited a strong escape response in the two species of freshwater copepods tested, which is consistent with the lack of bioluminescence and limited occurrence of shadow-casting predators that attack from above (cnidarian medusae) in fresh water systems.

Chemoreception in copepods is most commonly associated with their ability to identify and locate food (Buskey, 1984; Poulet & Marsot, 1978) and mates (Katona, 1973). Although there are several examples of studies demonstrating the importance of chemoreception of kairomones for predator avoidance in freshwater zooplankton, including copepods (Neill, 1990; Ringelberg, 1991), there have been fewer demonstrations of kairomone-mediated predator avoidance in marine zooplankton (e.g., Forward & Rittschof, 2000). Studies of the vertical migration pattern of the copepod *Acartia hudsonica* have concluded that chemical signals from planktivorous fish did not affect the vertical distribution of these copepods (Bollens, Frost, & Cordell, 1994.)

Like other crustaceans, copepods have many sensory sensilla on their appendages. In the calanoid copepods, the first antennae (= antennules) are long, often longer than the copepod and they extend perpendicular to the body. Mechanosensory, chemosensory, and mixed

modality setae have been identified based on morphological characteristics (Lenz, Weatherby, Weber, & Wong, 1996; Weatherby, Wong, & Lenz, 1994). The mechanoreceptors on the first antenna appear to be important for the detection of predators and prey (Gill, 1985; Hartline, Lenz, & Herren, 1996; Kiørboe & Visser, 1999; Landry, 1980), and they are highly sensitive (Hartline et al., 1996; Yen, Gassie, & Hartline, 1992). Physiological sensitivity and behavioral responses to mechanical stimuli extend to frequencies that are higher than reported for other crustacean mechanoreceptors (1 kHz; Hartline et al., 1996). Since high frequency hydrodynamic signals represent rapidly changing water motion, a characteristic shared with signals generated by sudden predatory lunges, this sensitivity seems likely to be an adaptation to enhance responsiveness to such attacks. Much of the research on mechanoreception of hydrodynamic disturbances has involved responses of copepods to artificial stimuli that mimic some aspects of the hydrodynamic disturbances created by natural predators, and the intensity of the signal is often near the lower threshold for detection, in order to determine sensitivity to specific stimuli (Burdick et al., 2007; Hartline et al., 1996). Escape responses may be stronger when copepods are exposed to larger and more complex hydrodynamic signals created by actual predators (Figure 1).

### 3 Myelinate and amyelinate copepods

In spite of their small size, calanoid copepods possess two adaptations in the nervous system that speed impulse conduction: giant axons and myelinated axons. Giant axons are found in all calanoids examined for this character (Lenz et al., 1996; Lowe, 1935; Park, 1966; Weatherby et al., 1994), where they have been interpreted as promoting rapid reactions in escape behavior. Myelin, derived from an unusual intraneuronal source (Wilson & Hartline, 2011a,b), has been consistently noted in axons of copepods from several superfamilies that contain about half of all described calanoid species (Davis, Weatherby, Hartline, & Lenz, 1999; Lenz, Hartline, & Davis, 2000; Weatherby, Davis, Hartline, & Lenz, 2000).

The response latency for escape jumps stimulated by hydrodynamic disturbances is among the most rapid found in nature, with response latencies as short as 2 ms between the initiation of a disturbance and the first motion of the escaping copepod (Buskey et al., 2002). Interestingly, the response latencies for escape jumps stimulated by photic stimuli are significantly longer, even though the escape responses are just as vigorous (Buskey & Hartline, 2003). Two factors that may affect the response latency of an organism to a defined stimulus are the distance over which a nervous signal must be conducted and the speed at which the signal is

propagated. The two main factors that affect the conduction speed of nervous signals are the diameter of a nerve fiber and whether or not that fiber is encased in a myelin sheath; for nerves of the same diameter, a myelin sheath increases the speed of signal conduction by an order of magnitude for fibers of a given diameter (Ritchie, 1984). To achieve the same conduction speed without a myelin sheath, the diameter of the nerve fiber would need to increase by a factor of 100 (Hartline & Coleman, 2007).

The increase in conduction velocity and mechanosensitivities to high frequencies suggest that these small invertebrates inhabit a world where time is crucial. Recent work by Gemmell (2011) sheds some light on the importance of time: the predatory attack of a sea horse takes approximately 1 ms, compared to a 2–3 ms response latency for a copepod escape jump, and the capture success rate of predators such as the sea horse is very high (90%; Gemmell, 2011). In contrast, planktonic larval fish capture success is much lower (<50%, 14-day-old *Amphiprion ocellaris* feeding on adult *Parvocalanus crassirostris*; Jackson, 2011), and millisecond differences in reaction times may determine the outcome of an attack.

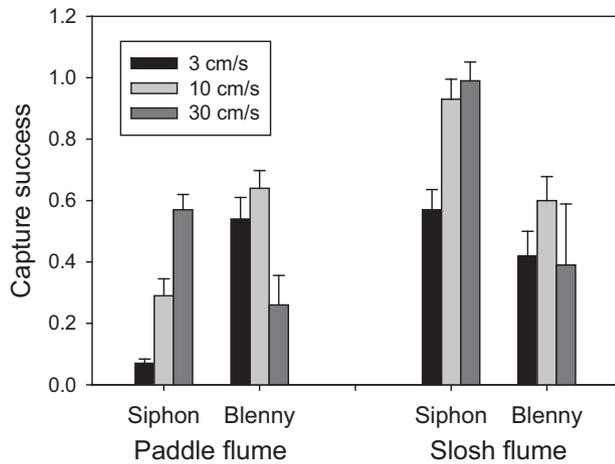
Studies of response latencies of copepods to abrupt hydrodynamic stimuli have typically used piezoelectric “pushers” that create rapid, very small, well controlled movements of a small sphere or cylinder immersed in water on the end of a small diameter rod (Lenz & Hartline, 1999; Lenz et al., 2000). Initial studies of reaction times of tethered copepods using a force transducer with a resolution in the tenths of a millisecond range demonstrated much shorter minimum response latencies among myelinate species (<2 ms) compared with amyelinate species (3–6 ms; Lenz et al., 2000). A subsequent study of numerous species of free swimming calanoid copepods using a more diffuse but abrupt stimulus, consisting of a single 1 ms sine wave pulse sent to an audio speaker in direct contact with the container housing the copepods, did not result in the same clear difference between the response latencies of myelinate and amyelinate species of copepods (Waggett & Buskey, 2008); however, the copepods studied were small and the temporal resolution of the video camera too coarse to clearly establish the level of differences expected. No clear relationships have been found between the presence of myelinated nerves in copepods and escape performance in terms of maximum or sustained escape swimming speeds (Waggett & Buskey, 2008).

#### 4 Effects of water motion on copepod–planktivore predator–prey interactions

Since the most important sensory modality for predator detection by copepods is through mechanoreception of hydrodynamic signals, it is reasonable that this

sensory capability will also depend on the hydrodynamic complexity of motion in the water column—the signal (predator approach) to noise (background water movements) ratio in the environment. It has long been recognized that turbulence has an important effect on encounter rates between planktivores such as larval fish and their copepod prey (Rothschild & Osborn, 1988), and that, while small amounts of turbulence may enhance the feeding rates of larval fish, too much turbulence may suppress capture rates of these predators (MacKenzie, Miller, Cyr, & Leggett, 1994). Small scale turbulence has been demonstrated to interfere with the ability of copepods to detect hydrodynamic signals associated with predator mimics such as siphons that draw water through a small diameter pipette (Gilbert & Buskey, 2005; Robinson, Finelli, & Buskey, 2007; Waggett & Buskey, 2007) as well as to interfere with the ability of copepods to detect the attacks of fish predators (Clarke, Buskey, & Marsden, 2005; Clarke, Finelli, & Buskey, 2009).

Since turbulence can affect both the ability of copepods to detect their predators and the ability of predators to capture prey, it is difficult to separate the effects of turbulence on predator–prey interactions. In laboratory experiments, the effects of water motion on planktivore feeding success were tested on both a predator-mimic (siphon) and a planktivorous fish (blenny) preying upon the copepod *Acartia tonsa* in the same flumes under two different flow conditions (Clarke et al., 2009; Robinson et al., 2007). The flow treatments were produced using a paddle flume, which produces unidirectional flow, and a slosh flume, which produces back-and-forth water motion (similar to that produced by surface waves). Three different water speeds, 3, 10, and 30 cm/s were tested; these speeds are within the range of those experienced by the planktivorous fish in their natural habitat (Finelli, Clarke, Robinson & Buskey, 2009). Although the maximum water speeds in the two flumes were similar, the reversing flow in the slosh flume produced much higher levels of turbulence compared with the continuous flow in the paddle flume. The different patterns of capture success (the proportion of copepods captured by the siphon or fish compared with the number of copepods encountered) demonstrated by the siphon and the fish, clarified the separate effects of water motion on the predator and its prey (Figure 3). For both flume types, the capture success of the siphon increased with increasing flow speeds. However, capture success with the siphon was consistently higher in the slosh flume than in the paddle flume at comparable speeds, suggesting that the copepods had more difficulty recognizing the flow signal associated with the siphon in the more turbulent flows of the slosh flume. The capture success of the blenny was higher than for the predator mimic (siphon) at flow speeds of 3 cm/s and 10 cm/s, but was lower than that of the siphon at 30 cm/s flow,



**Figure 3.** Comparison of capture success of the copepod *Acartia tonsa* by a predator mimic (siphon) and a fish predator, the coral reef blenny *Acanthemblemaria spinosa* at three different water speeds in a unidirectional paddle flume, or a slosch flume that simulates the oscillatory flow of surface waves. Error bars represent standard error. Data from Robinson et al. (2007) and Clarke et al. (2009).

indicating that the blenny's capture success was not negatively affected by water motion at the lower flow rates, but was impaired at the highest flow rate in spite of the reduced ability of copepods to detect their attacks (as indicated by their reduced response to the siphon at high flow). In the slosch flume, the capture success of the blennies shows a similar "domed response" with capture success increasing between the low flow and moderate flow conditions, but decreasing again at the highest flow speed. At all flow speeds in the slosch flume, the capture success of the blennies was less than that of the siphon for comparable speeds, indicating that the turbulence of the slosch flume had a negative effect on their ability to capture copepods, which was not compensated for by the reduced ability of the copepods to detect hydrodynamic disturbances.

## 5 Technical Challenges

Much remains to be learned about predator-prey interactions between planktonic copepods and their predators. Since these interactions occur on such short timescales (e.g., attack speeds and response latencies measured in milliseconds), high temporal resolution is essential to observe the details of these interactions. High speed video cameras are now readily available that can record at sub-millisecond resolution, but the higher the recording speed, the more light required to form images. Therefore, care must be taken to ensure that lighting in laboratory experiments does not affect the behavior of the organisms under study. These interactions also occur in three-dimensional spaces, and the spatial details of predators feeding on plankton often occur on the millimeter scale, requiring observations of

the predator's movements on a larger spatial scale and much finer spatial resolution of the details of the predator-prey interaction. Use of a plankton predator with limited movement, such as hemi-sessile blennies (Figure 1) or seahorses, makes it easier to predict the location where predator-prey interactions will occur (Clarke et al., 2005, 2009; Gemmell, 2011). However, even on these limited spatial scales, as magnification increases, depth of field of the image in focus becomes a limiting factor in spatial resolution of predator-prey interactions, especially for resolving interactions in three dimensions. One solution to this problem is to use either two cameras or mirrors and a single camera to observe a volume in three dimensions (Clarke et al., 2005, 2009). An emerging technology that addresses this problem is the use of holographic methods to reconstruct images and movements of organisms in three dimensions from a single camera (Sheng, Malkiel, & Katz, 2006). This requires video cameras with both high spatial and high temporal resolution, and specialized optics to produce coherent laser illumination. Holography has been successfully applied to studies of predation on copepods in the laboratory (Gemmell, 2011), and systems are under development that will allow for similar holographic observations underwater. These techniques also offer the advantage of being able to reconstruct the flow characteristics of surrounding water during a predator-prey interaction, allowing for estimation of the signal strength produced by fish during their attacks on copepods, and the amount of hydrodynamic disturbance needed to elicit escape responses to natural predators (Gemmell, 2011).

## 6 Conclusions

Copepods are the most abundant metazoans in the pelagic zone of the world's oceans. The majority of the photosynthetic primary production in the ocean comes from small single-celled phytoplankton that are largely grazed, either directly or indirectly, by copepods. These copepods are in turn consumed by a diverse assemblage of invertebrate and vertebrate predators. A variety of morphological, physiological, and behavioral adaptations have evolved to help individual copepods avoid becoming a part of this essential link in the oceanic food web. To fully understand the behavioral adaptations for avoiding predation, a better understanding of the neurophysiology and sensory physiology of these organisms is necessary. Great strides have been made in recent years in these areas, but much remains to be learned.

This food web supports open ocean fisheries that are suffering from overfishing and impacted in less well understood ways by pollution and global climate change. The planktonic community of the open ocean is incredibly diverse, with hundreds of species of phytoplankton and zooplankton coexisting in an oligotrophic

environment with low concentrations of nutrients to support plant growth and low standing stocks of primary producers to support the growth of primary and secondary consumers (McGowan & Walker, 1979). Attempts to directly model the complex interactions of oceanic food webs results in numerous simplifications that result in only modest, at best, improvement in the understanding of the factors affecting the structure and function of these complex communities. An understanding of the adaptations of copepods to avoid predation provides important insights into the ecological principles that govern the structure and function of oceanic food webs. Some adaptations, such as transparency and effective escape behaviors, allow copepods to remain in near surface waters during the day where the availability of food is greatest. Other adaptations, such as vertical migration, allow other copepod species to take refuge in the deeper, poorly lit and more oligotrophic waters during the day, and swim up into the more food rich surface waters at night. Other adaptations, such as bioluminescence allow deeper dwelling copepods to avoid visual predators in the dimly lit mesopelagic zone, where they feed on the rain of detritus from the productive photic zone. Copepods in all these habitats possess rapid escape behavior stimulated by hydrodynamics disturbances.

Many adaptations that help copepods avoid predation by active, visual predators may be ineffective against invertebrate predators including cnidarian medusae and ctenophores. The slow, hydrodynamically cryptic swimming behavior of these predators brings copepods into their “kill zone” of stinging cells or sticky surfaces without stimulating escape behavior (Waggett & Buskey, 2006). The wide variety of predators feeding on copepods, and the diverse adaptations of copepods to avoid predation may help explain the high diversity of copepods in the sea.

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