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Behavioral Characteristics of Copepods That Affect Their Suitability as Food for Larval Fishes

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ABSTRACT

Most fish larvae have evolved to feed selectively on complex natural assemblages of microzooplankton prey, and motion patterns are an important component in the recognition of particles as potential food items. This is why live (swimming) prey are often critical to the survival of larval fish. In response to fish predation many zooplankton species have also evolved adaptations to make them less visible to potential predators, including increased transparency and intermittent locomotion. In addition, calanoid copepods have evolved some of the most effective escape behaviors found among aquatic organisms. Some copepods can respond rapidly (< 3 milliseconds) to the slight hydrodynamic disturbance caused by an approaching predator, rapidly accelerating to speeds of up to 800 body lengths per second.

Part of the challenge in choosing copepod species for aquaculture applications is to select species that are easier for larval fish to recognize and that have less effective adaptations against small visual predators. Since copepods are preyed on by a wide array of predators ranging from protozoa to whales, they have evolved a wide variety of behaviors that may make some species less vulnerable to one type of predator but more vulnerable to others. In addition, environmental conditions, including light and turbulence, may modify the effectiveness of some of these adaptations. For example, many copepod species are difficult to see in light with a natural angular distribution (low image contrast), but become more easily visible under collimated illumination. In addition,

intermediate levels of turbulence not only increase encounter rates between predator and prey, but also inhibit escape responses of copepods through production of background hydrodynamic noise, which masks the approach of the predator, and through habituation of the copepods to small hydrodynamic disturbances.

INTRODUCTION

The science of rearing larval marine fish in captivity would be greatly simplified if marine fish larvae would readily consume artificial diets; the only challenge would be determining the nutritional requirements and correct size of particles for optimal growth of the species in question. Most fish larvae, however, have evolved to feed selectively on complex natural assemblages of zooplankton prey, and size, visibility, and motion patterns are important components in the recognition of particles as potential food items (Buskey et al. 1993). As a consequence, live (swimming) prey are often critical to the survival of larval fish (Watanabe et al. 1983). Many zooplankton species, however, have also evolved adaptations to avoid predation. Therefore, to successfully culture larval and juvenile fish, it is important to consider the factors affecting this predator-prey interaction and to choose conditions and prey species that favor the larval fish predator and maximize growth and survival of cultured species.

Artemia nauplii, which can be conveniently hatched from easily stored cysts, have been extensively used in larval fish culture (Leger et al.

1986). Due to the large size of *Artemia* nauplii, some fish species are first fed the easily cultured rotifer *Brachionus plicatilis* followed by *Artemia* nauplii. Supplementing *Artemia* diets with wild-collected zooplankton has led to better survival and growth of larval fish (e.g., Witt et al. 1984). These results have led to doubts regarding the nutritional suitability of *Artemia* for larval fish, especially in terms of its fatty acid composition (Watanabe et al. 1983), and raised interest in copepods as a potential alternative food for rearing larval fish. In nature, copepods are a major dietary component for marine fish larvae (May 1970; McMichel and Peten 1989). They have also been used in aquaculture as food for marine fish larvae (Houde 1973) and have proven a superior food source for rearing fish and crustaceans in intensive culture (Watanabe et al. 1983; Støttrup and Norsker 1997; McEvoy et al. 1998). The great number of species and sizes potentially available for aquaculture (Delbare et al. 1996) is further evidence of their suitability as a food source.

Cultivation of planktonic copepod species, mainly calanoids, has generally been limited in practical application by the low densities achieved in culture (Støttrup and Norsker 1997). Although species that protect their eggs by carrying them in clusters may experience lower mortality (Kiørboe and Sabatini 1994), in general, copepod species that free-spawn their eggs have higher fecundity than species in which females carry their eggs in clusters (Mauchline 1998). Overcrowding can decrease fecundity in some species (Miralto et al. 1996) or result in cannibalism of nauplii (Lonsdale et al. 1979; Ohno et al. 1990). While harpacticoid copepods have been cultured in high densities, their benthic nature may make them less readily available to fish larvae. The nauplii of some harpacticoids, however, exhibit positive phototaxis, compared to the negative phototaxis of adults, making them easy to harvest from the surface layers of a culture (Strøttup and Norsker 1997). Recent studies with the swarm-forming cyclopoid copepod *Dioithona oculata* suggest that this species may be a good candidate for high-density culture (Hernandez Molejon and Alvarez-Lajonchere 2003). This species lives in swarms that can reach densities of over 50,000 copepods/L (Buskey et al. 1996).

While the major factors affecting the decision

of which copepod species to culture for aquaculture applications have rightfully centered around their ease of culture and potential for mass culture, it is also worthwhile to consider the behavioral characteristics of various copepod species and how these characteristics may affect their availability as prey to larval fish. A wide range of predators feed on copepods, ranging from protozoa to whales (Greene 1985), and the adaptations that help protect copepods from one type of predator might be ineffective against other groups of predators. Copepod predators can be classified in several ways. There are active predators, such as fish that seek out their prey, and passive predators, such as corals or jellyfish that rely on copepods swimming into tentacles or being carried there by currents. Active predators can also be classified by the dominant sensory systems used to locate prey, making for a natural division between visual and nonvisual predators. Most planktivorous fish are visual predators (Hunter 1981; Blaxter 1991) that feed on individual prey by rapidly sucking in the water surrounding them (Lauder 1983), although a few species of planktivorous fish may feed primarily by filtering plankton from the water (Durbin and Durbin 1975); some species are capable of both feeding modes (e.g., O'Connell 1972) or switch between them during ontogeny (e.g., Drenner et al. 1982a). Visual predators typically feed selectively on the largest and most conspicuous zooplankton species, based on body size, pigmentation, and prey motion (Brooks and Dodson 1965; Zaret and Kerfoot 1975; Zaret 1980). For filter-feeding fish, it might be expected that these planktivores would randomly sample their food environment within a particular size range determined by the morphology of their feeding structures. Prey avoidance, however, can significantly alter prey selection in filter-feeding fish, causing them to feed more successfully on smaller, less evasive prey (Drenner and McComas 1980; Drenner et al. 1982b).

Fish are often not the dominant predators on zooplankton (Cushing 1983; Bollens 1988; Dagg and Govoni 1996). Therefore, invertebrate predators may be a major selective force in the evolution of antipredator adaptations, and their impact on copepod populations must be considered at least briefly. Under some circumstances invertebrates may be the dominant predators on zoo-

plankton in marine environments (e.g., Ohman 1986; Behrends and Schneider 1995) and may therefore play an important role in the evolution of antipredator adaptations. Invertebrate predators on zooplankton can be distinguished as either cruising or ambush predators (Greene 1985). Cruising predators tend to prey upon slow-moving prey, while ambush predators, which rely on the swimming behavior of the prey to initiate encounters (Gerritsen 1978), tend to favor prey with higher swimming speeds. Invertebrate predators can also be characterized according to the means by which they capture their prey (i.e., raptorial versus entangling predators). Although some raptorial invertebrate planktivores rely upon vision to locate prey (e.g., crustaceans with compound eyes and good visual acuity), many rely upon mechanoreception (e.g., chaetognaths [Newbury 1972] and predatory copepods [Strickler 1975]). Thus the encounter radius for the predator can be defined by its optical or mechanosensory range, resulting in selection for more visually or hydrodynamically (respectively) conspicuous prey. The encounter radius for entangling predators, on the other hand, is defined by the volume occupied by tentacles (Madin 1988). In those systems where they are the dominant predators on zooplankton (e.g., Kremer 1979; Deason 1982; Purcell 1992), entangling predators may favor prey with higher swimming speeds and therefore higher encounter rates with predators.

Zooplankton that have evolved in extreme or temporary habitats are often exposed to fewer predators, and, as a consequence, may have evolved fewer adaptations to avoid predation. In addition, they may also be easier to culture because of their adaptations to extreme or changing environments. For example, the brine shrimp *Artemia salina* is widely used as live food in large part because it is easily raised from dormant cysts, has broad tolerance to varying temperature and salinity conditions, and has the added advantage of being a highly visible prey with virtually no escape behavior (Buskey et al. 1993). Similarly, tide pool copepods, such as the harpacticoid *Tigriopus californicus*, are often easier to culture than many coastal marine species (Fukusho 1980), in part because of their tolerance to highly fluctuating tide pool environments. Cyclopoid copepods of the genus *Apocyclops*, which are characteristic of coastal saline pools and ponds

(Reid et al. 2002), are also extremely easy to culture (Buskey unpublished data) and may be of value in aquaculture (James and Al-Khars 1986).

To understand the characteristics that make a copepod species suitable for larval fish culture, it is advantageous to consider the biology and ecology of the predator-prey interactions between larval and juvenile fish and copepods. A convenient framework for considering this interaction is to consider the four primary components of a predator-prey interaction (encounter, attack, capture, and ingestion) as suggested by Holling (1959) (see, for example, Gerritsen and Strickler 1977; Greene 1983; Ohman 1988). By studying each of these components and the biological and environmental factors that affect them, a better understanding of the overall predator-prey interaction may be gained.

FACTORS AFFECTING ENCOUNTER PROBABILITY

For a predator-prey interaction to occur, the predator must encounter the prey either through direct contact with feeding structures or by remotely detecting its prey using one or more sensory systems. Gerritsen and Strickler (1977) modeled the factors affecting predator-prey encounter rates in aquatic systems, including the speed of the predator, the speed of the prey, and the distance at which a predator is able to detect the presence of prey (encounter radius). In its simplest form this model assumes a random distribution of prey, random swimming direction, and no water motion. Of the variables used in this model (population density, speeds of predator and prey, encounter radius), encounter radius has the greatest effect on encounter probabilities. In a later study examining the effects of swimming direction, it was determined that cruising predators can maximize their encounter rates by swimming orthogonally to the predominant prey direction, while prey can minimize their encounter rates by swimming parallel to predators (Gerritsen 1980). This encounter model was later modified to include the effects of turbulent mixing on encounter rates (Rothschild and Osborn 1988).

In calculation of encounter rates, predator and prey movement speeds are theoretically of equal importance. Larval fish are primarily cruising raptorial feeders whose routine swimming speeds

are often in the range of one to three body lengths per second (Miller et al. 1988). Their copepod prey have similar swimming speeds (in terms of body length), ranging from less than one to about five body lengths per second (summarized in Mauchline 1998). Since copepods are generally much smaller than their fish predators, their absolute swimming speeds are generally much lower than those of their predators, and prey swimming speeds have relatively little effect on encounter rates. This is especially true for early naupliar stages of copepods, which (due to their small size) would be the logical choice as food for larval fish in aquaculture applications. For copepods there is a general pattern of increased swimming speed with both body size and developmental stage (Fig. 8.1). Early naupliar stages of copepods are often nonfeeding (Gauld 1959; Marshall 1973); in some genera (mainly deep sea or predatory species), none of the naupliar stages feed (Sekiguchi 1974). These nonfeeding developmental stages tend to conserve energy reserves and make themselves less conspicuous to predators by swimming less vigorously than feeding nauplii; very low swimming speeds have generally been found among early naupliar stages of copepods (Gerritsen 1978).

Another factor that may affect encounter fre-

quencies is an uneven, heterogeneous distribution of prey. Early studies of larval fish feeding emphasized the concept that certain minimum thresholds of food concentration were necessary for the survival of larval fish and that these often occurred in spatially limited, high-density patches, such as the chlorophyll maximum layer (Lasker 1975). Taken to the extreme, however, exceptionally high prey densities, such as copepod swarms, may have a negative impact on visual predators such as larval fish. Dense swarms of copepods have been reported from a wide range of marine habitats, including coastal bays, coral reefs, and among mangrove prop roots (Emery 1968; Ueda et al. 1983; Ambler et al. 1991). Even *Artemia*, an important food item for rearing larval fish, is known to form swarms within culture tanks (Gulbrandsen 2001), which in turn affects ingestion rates of larval fish (Gulbrandsen 1996). The adaptive value of swarming behavior to copepods is thought to include enhanced mating opportunities, reduced dispersion by currents, and protection from predators (Hamner and Carlton 1979).

Although aggregated prey may initially be more conspicuous to visual predators (Vine 1973; Treisman 1975), especially within the confines of a tank for rearing larval fish, feeding on individ-

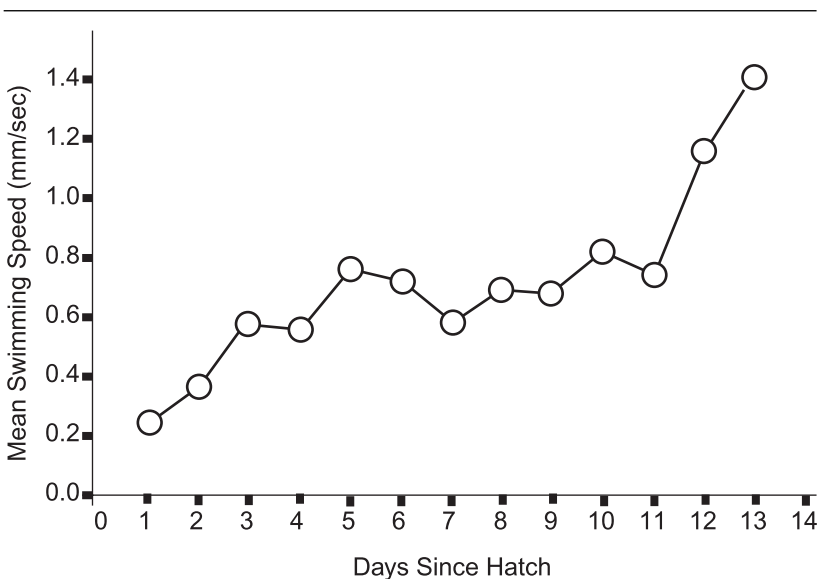


Figure 8.1. Changes in mean swimming speed over the developmental stages of the calanoid copepod *Acartia tonsa* from naupliar stage NI on day 1 through adult copepods on day 13. From Buskey (1994) with permission of Kluwer Academic Publishers.

ual prey within a swarm may be more difficult than feeding on isolated individuals because of the confusion effect caused by a great number of uniform moving targets (Neill and Cullen 1974). This confusion effect is enhanced by increasing the number of individuals in an aggregation (Neill and Cullen 1974), through high density within a swarm (Millinski 1977a, 1977b; Morgan and Ritz 1984), and by uniformity of individuals within a swarm, since visually conspicuous swarm members are most at risk (Ohguchi 1978). While swarming behavior may be an effective defense against visual planktivores, it may make them more vulnerable to nonvisual entangling predators such as cubozoan medusae that can use photobehavior to locate swarms (Buskey 2003).

Turbulence may also have an important effect on encounter rates between planktonic predators and their prey. Early attention was given to the role of vertical mixing in breaking down patchy areas of high food concentration, which in turn could lead to decreased feeding and survival of fish larvae (Lasker 1975). Rothschild and Osborn (1988) modeled the effects of turbulence on contact rates between planktonic organisms as an extension of the encounter rate model of Gerritsen and Strickler (1977). Mackenzie et al. (1994) modeled the effects of wind-induced turbulence on encounter rates between fish larvae and their prey and on capture success of prey by larval fish. They predicted a dome-shaped relationship for the effects of turbulence on feeding rate, with moderate levels of turbulence leading to the greatest enhancement of feeding rate. Field studies have confirmed the role of moderate turbulence in enhancing the feeding rates of larval fish (e.g., Sundby et al. 1994).

FACTORS AFFECTING ATTACK PROBABILITY

What characteristics of zooplankton prey cause them to be recognized as potential food for larval fish? Most predator–prey interactions in the plankton that involve remote detection of prey are mediated through vision or mechanoreception. There is relatively little evidence for chemoreception being involved in detection of zooplankton prey, although there is evidence for its use in mate location among copepods (Katona 1973). Larval and juvenile fish are primarily diurnal, visual pre-

dators (Hunter 1981), and feed selectively when presented with prey choices (e.g., Checkley 1982; Govoni et al. 1986), indicating that certain prey characteristics are more likely to induce attacks by larval fish.

Prey size has been widely recognized as an important factor in the feeding of planktivorous fish. Since Brooks and Dodson (1965) demonstrated body size–related predation by planktivorous fish, there has been a wealth of information published on this aspect of visual predation on zooplankton prey. In general, preferred prey organisms lie within a size range that varies with fish species and size, below which prey are too small either to be seen or to be energetically profitable to consume and above which there are physical limitations to prevent ingestion. For example, *Artemia* nauplii are too large for first-feeding larvae of some species to ingest, but small enough to escape detection by larger fish. Copepod nauplii occur in a wide range of sizes, with copepod species that carry eggs producing relatively larger eggs and nauplii than those species that free-spawn their eggs (Kiørboe and Sabatini 1994).

In addition to size, there is also evidence that both illumination and prey contrast can affect the feeding and growth of larval and juvenile fish (Vinyard and O'Brien 1976; Hinshaw 1985). Some zooplankton species are nearly transparent, and only the portions of their bodies with increased pigmentation may be visible (Zaret 1972; Zaret and Kerfoot 1975). The first, nonfeeding naupliar stages of copepods may have significantly lower image contrast than older feeding stages (Fig. 8.2). For zooplankton that live near the surface in clear waters, there may be a trade-off between increased risk of damage from ultraviolet light due to low pigmentation and higher risk of predation if protective pigments are produced (Hansson 2000). The distance at which prey are visible underwater depends on prey size, image contrast, ambient illumination, and the turbidity of the water (Eggers 1977; Aksnes and Giske 1993; Aksnes and Utne 1997). Because nearly transparent zooplankton have low image contrast when viewed against a bright background, planktivorous fish can enhance the contrast of their prey by searching for them at angles greater than 48.6 degrees from the vertical, which places their image just outside of Snell's window and makes them appear bright against a dark

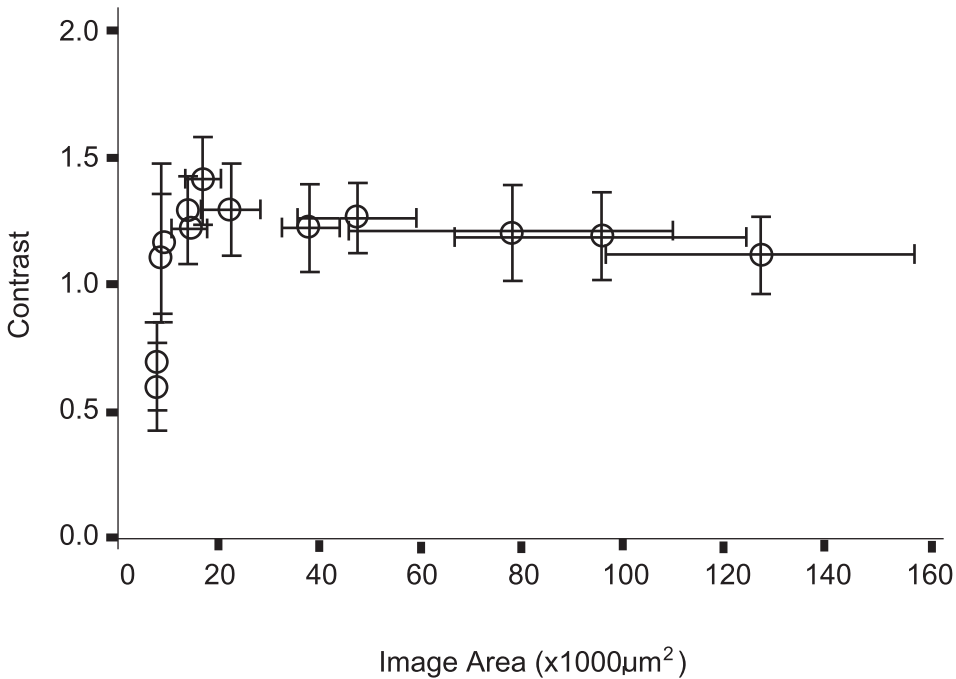


Figure 8.2. Changes in image area (visible size) and image contrast (image brightness minus background brightness, divided by background brightness) over developmental stages for the calanoid copepod *Acartia tonsa*, over 13 days of development from naupliar stage NI through adult. From Buskey (1994) with permission of Kluwer Academic Publishers.

background, similar to observing them under dark-field illumination with a microscope (Janssen 1981).

In coastal bays and estuaries, where the density of nonfood particles is very high, zooplankton prey may be difficult to recognize, based on size and image contrast alone. There is increasing evidence that prey recognition by planktivores may be strongly influenced by prey movement (Zaret 1980; Wright and O'Brien 1982). The steady, jerky swimming of *Artemia* nauplii appear to make it easily recognized as food by a wide range of larval fish. Most copepod nauplii exhibit intermittent locomotion (Buskey et al. 1993), with periods of jerky swimming interspersed with periods of quiescence (Fig. 8.3). This behavior pattern may not only make it more difficult for visual predators to keep track of their prey, but may also allow the nauplii to detect the approach of predators using mechanoreception during periods of no motion (Kramer and McLaughlin 2001). The activity levels of copepod nauplii differ greatly among species, and this may influence their con-

spicuousness as food for larval fish. For example, nauplii of *Parvocalanus crassirostris* hop with a frequency of about once per second, while nauplii of *Oithona plumifera* often go for periods of up to 10 seconds without moving (Buskey et al. 1993). In general, it would be expected that copepod nauplii with more continuous swimming behavior would be more easily recognized as prey by larval fish.

While there is considerable evidence that mechanoreception plays an important role in predation on zooplankton by invertebrate predators (e.g., Yen and Strickler 1996), the role of mechanoreception in predation by larval fish is less clear. There is evidence that some species of juvenile and adult fish feed raptorially on zooplankton in the dark, based on mechanoreception of hydrodynamic signals by the lateral line (Montgomery and Saunders 1985; Montgomery 1989; Janssen et al. 1995), as well as evidence that some species filter feed in the dark (Batty et al. 1986). There is also evidence that larval fish use their developing lateral line to detect zooplankton in the dark (Batty

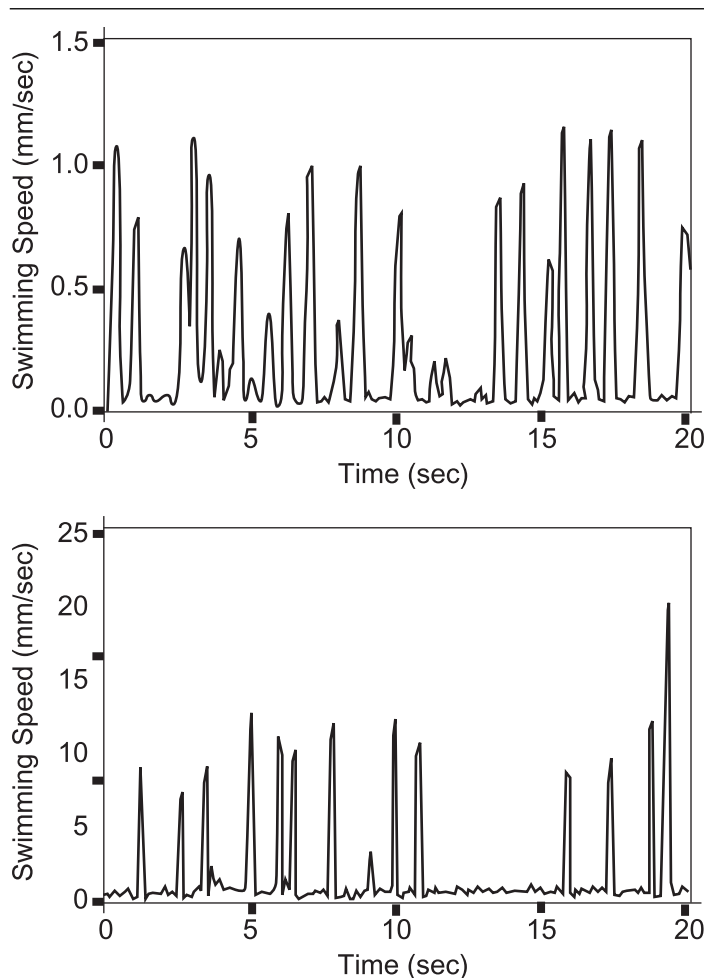


Figure 8.3. Representative records of swimming speed over time for the calanoid copepod *Acartia tonsa* NI nauplius (top panel) and adult female (bottom panel). Both stages exhibit a highly conspicuous, intermittent swimming pattern. From Buskey (1994) with permission of Kluwer Academic Publishers.

and Hoyt 1995; Salgado and Hoyt 1996), but the importance of this feeding mode and the extent to which it is used in various species of larval fish needs further study. Conditions that favor visual predation of fish larvae, along with prey possessing high visual conspicuousness, should lead to highest feeding rates in aquaculture applications.

FACTORS AFFECTING CAPTURE PROBABILITY

Once a copepod has been detected and attacked by a larval fish, the probability of capture is affected primarily by the escape behavior of the

copepod. The vigorous escape behaviors of copepods represent important adaptations for avoiding predation and may play an important role in the selective feeding of planktivores (Drenner et al. 1978). These escape responses can be elicited by hydrodynamic (Hartline et al. 1999; Kiørboe et al. 1999; Lenz and Hartline 1999) and photic stimuli (Buskey et al. 1986; Buskey and Hartline 2003). It is generally accepted that water deformation is the primary effective stimulus to elicit an escape response by copepods (Haury et al. 1980; Yen et al. 1992; Kiørboe and Visser 1999). Rapid changes in light intensity (such as caused by a shadow during the day) or rapid increases in

light intensity (such as the flash of a bioluminescent organism at night) trigger photophobic escape responses (Buskey et al. 1987). Chemosensory detection of predators by copepods may cause a reduction in swimming activity, perhaps making them less easily detected by planktivorous fish (Van Duren and Videler 1996), but chemoreception does not directly stimulate escape behavior.

Several factors may determine the effectiveness of copepod escape responses, including sensitivity to hydrodynamic stimuli, response latencies, and kinetic characteristics of the escape jump itself (Buskey et al. 2002). Several studies have attempted to determine hydrodynamic sensitivity thresholds (Viitasalo et al. 1998; Kiørboe and Visser 1999), but information on threshold sensitivity to hydrodynamic disturbances is only available for a small number of copepod species at present. Preliminary studies indicate that there are pronounced differences in hydrodynamic sensitivity among copepods (Fields and Yen 1997; Waggett and Buskey, unpublished data). There appears to be little change in sensitivity to hydrodynamic stimuli with increasing age and developmental state for nauplii and early copepodids of *Acartia tonsa*; the distance at which they respond to a standardized siphon flow is similar for all naupliar stages, although an increase in sensitivity is observed during the transition from the last naupliar stage (NVI) to the first copepodid stage (Fig. 8.4). Sensitivity thresholds are affected by the amount of ambient hydrodynamic noise in the environment, and escape responses may be reduced due to habituation in highly turbulent conditions (Hwang et al. 1994). Recent studies have demonstrated that planktivorous fish with low success capturing evasive prey (copepods) and high success at capturing nonevasive prey (*Artemia*) under still water conditions increase their success at capturing evasive prey and decrease their success at capturing nonevasive prey under turbulent conditions (Clarke et al., unpublished). This suggests that turbulence is either providing too much background noise for the copepod to distinguish the hydrodynamic signal associated with the approach of the predator or that the copepod has habituated to all small hydrodynamic fluctuations and does not respond to the predator's approach. Therefore, addition of moderate levels of turbulence to larval rearing tanks might increase the encounter rates

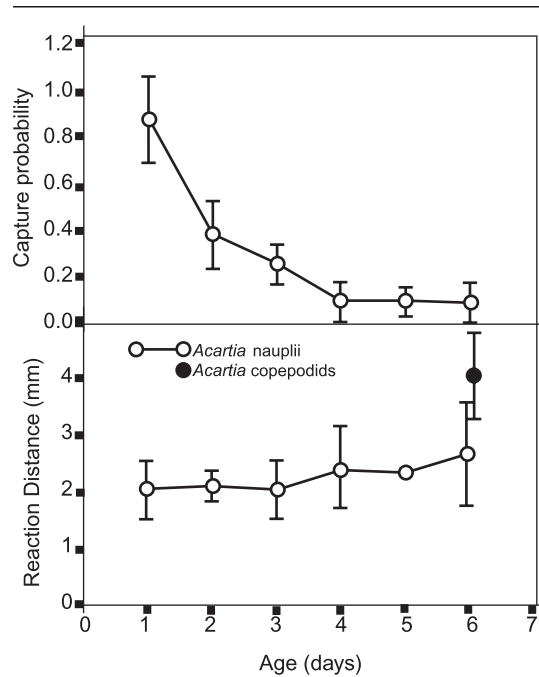


Figure 8.4. Changes with development in capture probability of *Acartia tonsa* naupliar stages by a siphon tube from NI nauplii on day 1 to NVI nauplii on day 6 (top panel), and mean reaction distance for nauplii exhibiting escape responses (bottom panel). Capture probability decreases with naupliar development, with little change in reaction distance, indicating that the strength of escape responses is increasing rapidly with development. From Buskey (1994) with permission of Kluwer Academic Publishers.

between predator and prey (MacKenzie et al. 1994; Sundby 1997) as well as reduce the ability of prey to detect their predators.

The time delay between the stimulus and behavioral response is a critical component of the escape response of an organism. Extremely short latencies (< 1 millisecond) to the first preparatory movement of an escape response to hydrodynamic stimuli have been demonstrated in copepods possessing myelinated nervous systems (Davis et al. 1999; Lenz and Hartline 1999; Lenz et al. 2000). These are among the fastest response times recorded for animals (Lenz et al. 2000) and are faster than even the Mauthner-mediated fast start reaction in adult zebra fish (5 milliseconds) (Eaton et al. 1977). Response latencies to photic stimuli are considerably longer; for adult *A. tonsa*, the minimum response latency to a hydrodynamic stimulus is 2 milliseconds (Buskey et al.

2002), while the minimum response latency to a photic stimulus is 30 milliseconds (Buskey and Hartline 2003). Visual response latencies for small fish are also approximately 30 milliseconds, providing a response time advantage to copepods that detect the approach of their predators with hydrodynamic signals over predators that detect their prey visually. Although fewer studies have focused on response latencies of early developmental stages of copepods, recent evidence indicates that response latencies to hydrodynamic stimuli are significantly longer for copepod nauplii than for adult stages. For example, the response latency to a hydrodynamic disturbance for a first naupliar stage *A. tonsa* averages about 27 milliseconds, compared to about

3.5 milliseconds for adults (Buskey et al. 2002; unpublished data).

In addition to quick response times, copepods also have extremely vigorous escape responses that are among the fastest of any aquatic organisms (Fig. 8.5). Maximum escape speeds of up to 840 mm/sec (approximately 800 body lengths/sec) have been recorded for the copepod *Acartia lilljeborgii*, with maximum accelerations exceeding 300 m/sec (Buskey et al. 2002). This compares with maximum-burst swimming speeds that can be as high as 400 mm/sec (approximately 80 body lengths/sec) for small larval fish (Williams et al. 1996). Copepod escape jumps are also characterized by a rapid initial change in direction of about 50 degrees (but ranging from 0 to 180 degrees;

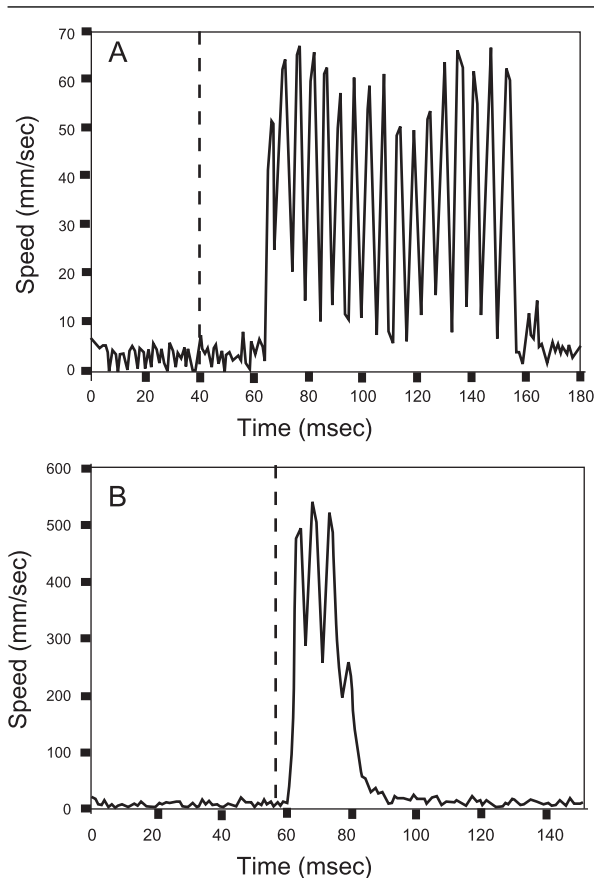


Figure 8.5. Representative records of swimming speed over time for escape responses of *A. tonsa* NI nauplius (top) and adult (bottom), based on high-speed video recordings at 1,000 frames per second. Vertical dashed line indicates onset of hydrodynamic stimulus. Bottom graph from Buskey et al. (2002) with permission of Inter-Research Science Publisher.

Buskey et al. 2002). This may make it very difficult for visual predators to anticipate the direction of the escape trajectory. Less is known about the detailed kinetics of escape responses of copepod nauplii, but they have effective escape responses to hydrodynamic stimuli (Yen and Fields 1992) and the effectiveness of their escape behavior increases with developmental stage, due mainly to an increase in the vigor of the escape response (Buskey 1994). While the maximum escape speeds of copepod nauplii are considerably slower than those found for adults (about 60 mm/sec for NI *A. tonsa* nauplii; Fig. 8.5), they are similar to adult speeds when scaled to their size (600 body lengths/sec for a 0.1-mm *A. tonsa* NI and 500 body lengths/sec for a 1-mm adult *A. tonsa*; Buskey et al. 2002). While the motion kinetics of escape behavior are well characterized for only a limited number of copepod species, as more species are studied, it is expected that a wide range of escape characteristics will be found among copepod species. For example, the swarm-forming copepod *D. oculata*, while a very active swimmer, seems to lack the capability for the vigorous escape response found in most planktonic copepod species (Buskey, unpublished data). When choosing copepod species for aquaculture, those with less effective escape behaviors might be favored.

FACTORS AFFECTING INGESTION

Once prey have been attacked and captured, there is still a small probability that the predator may reject the prey and release it. The reasons for prey rejection could include size (too big to ingest), morphological adaptations such as spines to deter predation, or chemical adaptations to make the prey toxic or unpalatable.

There are numerous examples of morphological adaptations to avoid predation among freshwater zooplankton, including spines on rotifers and helmets on cladocerans that are induced by the presence of predators (e.g., Stemberger and Gilbert 1987; Tollrian 1995). Although spination is a common characteristic of many marine planktonic organisms, spines have only rarely been shown to effectively deter predation by fish; for example, the prominent spines of crab zoea (Morgan 1989) and the setae of polychaete trocho-

phores (Pennington and Chia 1984). Although planktonic copepods generally do not have sufficiently formidable spines to serve in an antipredator function, some harpacticoid copepods have stout, elongated caudal setae that cause planktivorous fish to reject them after capture (Buskey, unpublished data). There are no known reports of chemical defenses in copepods that would make them poisonous or distasteful to their predators. Chemical defenses have been found in marine invertebrate larvae (Lindquist and Hay 1996) and freshwater zooplankton (Kerfoot 1982).

CONCLUSION

While the ease of establishing highly productive cultures will be the main factor affecting the choice of copepod species to act as food for rearing of marine fish larvae, an awareness of the physical and behavioral characteristics of copepods that affect their ability to avoid predation, as well as environmental factors that reduce the effectiveness of antipredator characteristics, may lead to enhanced feeding rates of fish larvae and improved survival and growth. Copepod species from harsh or temporary environments may have wide environmental tolerances and lack sophisticated antipredator adaptations. Environmental conditions in larval rearing tanks may also be optimized in terms of lighting that provides high-contrast images of zooplankton and water circulation to provide enough turbulence to both increase encounter rates and deter escape responses of prey. These modifications may defeat some predator avoidance adaptations in copepods and enhance feeding rates of larvae.

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REFERENCES

- Ambler, J.W., Ferrari, F.D., and Fornshell, J.A. 1991. Population structure and swarm formation of the copepod *Dioithona oculata* near mangrove cays. *Journal of Plankton Research* 13:1257–1272.

- Aksnes, D.L. and Giske, J. 1993. A theoretical model of aquatic visual feeding. *Ecological Modeling* 67:233–250.
- Asknes, D.L. and Utne, A.C.W. 1997. A revised model of visual range in fish. *Sarsia* 82:137–147.
- Batty, R.S., Blaxter, J.H.S., and Libby, D.A. 1986. Herring (*Clupea harengus*) filter-feeding in the dark. *Marine Biology* 91:371–375.
- Batty, R.S. and Hoyt R.D. 1995. The role of sense organs in the feeding behavior of juvenile sole and plaice. *Journal of Fish Biology* 47:931–939.
- Behrends, G. and Schneider, G. 1995. Impact of *Aurelia aurita* medusae (Cnidaria, Scyphozoa) on the standing stock and community composition of mesozooplankton in the Kiel Bight (western Baltic Sea). *Marine Ecology Progress Series* 127:39–45.
- Blaxter, J.H.S. 1991. Sensory systems and behavior of larval fish. In *Marine Biology: Its Accomplishment and Future Prospect*, edited by J. Mauchline and T. Nemoto, pp. 15–38. New York, New York, USA: Elsevier.
- Bollens, S.M. 1988. A model of the predatory impact of larval marine fish on the population dynamics of their zooplankton prey. *Journal of Plankton Research* 10:887–906.
- Brooks, J.L. and Dodson, S.I. 1965. Predation, body size and composition of plankton. *Science* 150:28–35.
- Buskey, E.J. 1994. Factors affecting feeding selectivity of visual predators on the copepod *Acartia tonsa*: locomotion, visibility and escape responses. *Hydrobiologia* 292/293:447–453.
- Buskey, E.J. 2003. Behavioral adaptations of the cubozoan medusa *Tripedalia cystophora* for feeding on copepod (*Dioithona oculata*) swarms. *Marine Biology* 142:225–232.
- Buskey, E.J., Coulter, C.J., and Strom, S.L. 1993. Locomotory patterns of microzooplankton: potential effects on food selectivity of larval fish. *Bulletin of Marine Science* 53:29–43.
- Buskey, E.J. and Hartline, D.K. 2003. High-speed video analysis of the escape responses of the copepod *Acartia tonsa* to shadows. *Biological Bulletin* 204:28–37.
- Buskey, E.J., Lenz, P.H., and Hartline, D.K. 2002. Escape behavior of planktonic copepods in response to hydrodynamic disturbances: high speed video analysis. *Marine Ecology Progress Series* 235:135–146.
- Buskey, E.J., Mann, C.G., and Swift, E. 1986. The shadow response of the estuarine copepod *Acartia tonsa*. *Journal of Experimental Marine Biology and Ecology* 103:65–75.
- Buskey, E.J., Mann, C.G., and Swift, E. 1987. Photophobic responses in calanoid copepods: possible adaptive value. *Journal of Plankton Research* 9:857–870.
- Buskey, E.J., Peterson, J.O., and Ambler, J.W. 1996. The swarming behavior of the copepod *Dioithona oculata*: in situ and laboratory studies. *Limnology and Oceanography* 41:513–521.
- Checkley, D.M. 1982. Selective feeding by Atlantic herring (*Clupea harengus*) larvae on zooplankton in natural assemblages. *Marine Ecology Progress Series* 9:245–253.
- Cushing, D.H. 1983. Are fish larvae too dilute to affect the density of their prey? *Journal of Plankton Research* 5:847–854.
- Dagg, M.J. and Govoni, J.J. 1996. Is ichthyoplankton predation an important source of copepod mortality in subtropical coastal waters? *Marine and Freshwater Research* 47:137–144.
- Davis, A.D., Weatherby, T.M., Hartline, D.K., and Lenz, P.H. 1999. Myelin-like sheaths in copepod axons. *Nature* 398:571.
- Deason, E.E. 1982. *Mnemiopsis leidyi* (Ctenophora) in Narragansett Bay, 1975–1980: Abundance, size composition and estimation of grazing. *Estuarine, Coastal and Shelf Science* 15:121–134.
- Delbare, D., Dhert, P., and Lavens, P. 1996. Zooplankton. In *Manual on the Production and Use of Live Food for Aquaculture*, edited by P. Lavens and P. Sorgeloos, pp. 252–282. FAO Fisheries Technical Papers, No. 361. Rome, Italy: Food and Agriculture Organization of the United Nations.
- Drenner, R.W., de Noyelles, F., Jr., and Kettle, D. 1982a. Selective impact of filter feeding gizzard shad on zooplankton community structure. *Limnology and Oceanography* 27:965–968.
- Drenner, R.W. and McComas, S.R. 1980. The role of zooplankton escape ability and fish size selectivity in the selective feeding and impact of planktivorous fish. In *Evolution and Ecology of Zooplankton Communities*, edited by W.C. Kerfoot, pp. 587–593. Hanover, New Hampshire, USA: University Press of New England.
- Drenner R.W., Strickler, J.R., and O'Brien, W.J. 1978. Capture probability: the role of zooplankton escape in the selective feeding of planktivorous fish. *Journal of the Fisheries Research Board of Canada* 35:1370–1373.
- Drenner, R., Vinyard, G.L., Gophen, M., and McComas, S.R. 1982b. Feeding behavior of the cichlid *Sarotherodon galilaeum*: selective predation on Lake Kinneret zooplankton. *Hydrobiologia* 87:17–20.
- Durbin, A.G. and Durbin, E.G. 1975. Grazing rates of the Atlantic menhaden *Brevoortia tyrannus* as a function of particle size and concentration. *Marine Biology* 33:265–277.

- Eaton, R.C., Bombardieri, R.A., and Meyer, D.L. 1977. The Mauthner-initiated startle response in teleost fish. *Journal of Experimental Biology* 66:65–81.
- Eggers, D.M. 1977. The nature of prey selection by planktivorous fish. *Ecology* 58:46–59.
- Emery, A. 1968. Preliminary observations of coral reef plankton. *Limnology and Oceanography* 13:293–303.
- Fields, D.M. and Yen, J. 1997. The escape behavior of marine copepods in response to a quantifiable fluid mechanical disturbance. *Journal of Plankton Research* 19:1289–1304.
- Fukusho, K. 1980. Mass production of a copepod, *Tigriopus japonicus*, in combination culture with a rotifer *Brachionus plicatilis*, fed yeast as a source. *Bulletin of the Japanese Society of Scientific Fisheries* 46:625–629.
- Gauld, D.T. 1959. Swimming and feeding in crustacean larvae: the nauplius larva. *Proceedings of the Zoological Society of London* 132:31–50.
- Gerritsen, J. 1978. Instar-specific swimming patterns and predation of planktonic copepods. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 20:2531–2536.
- Gerritsen, J. 1980. Adaptive responses to encounter problems. In *Evolution and Ecology of Zooplankton Communities*, edited by W.C. Kerfoot, pp. 52–62. Hanover, New Hampshire, USA: University Press of New England.
- Gerritsen, J. and Strickler, J.R. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. *Journal of the Fisheries Research Board of Canada* 34:73–82.
- Govoni, J.J., Ortner, P.B., Al Yamani, R., and Hill, L.C. 1986. Selective feeding of spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonius undulatus*, larvae in the northern Gulf of Mexico. *Marine Ecology Progress Series* 28:175–183.
- Greene, C.H. 1983. Selective predation in freshwater zooplankton communities. *International Review of Hydrobiology* 68:297–315.
- Greene, C.H. 1985. Planktivore functional groups and patterns of prey selection in pelagic communities. *Journal of Plankton Research* 7:35–40.
- Gulbrandsen, J. 1996. Effects of spatial distribution of light on prey ingestion of Atlantic halibut larvae (*Hippoglossus hippoglossus* L.). *Journal of Fish Biology* 48:478–483.
- Gulbrandsen, J. 2001. *Artemia* swarming — mechanisms and suggested reasons. *Journal of Plankton Research* 23:659–669.
- Hamner, W.M. and Carlton, J. 1979. Copepod swarms: attributes and role in coral reef ecosystems. *Limnology and Oceanography* 24:1–14.
- Hansson, L.-A. 2000. Induced pigmentation in zooplankton: A trade-off between threats from predation and ultraviolet radiation. *Proceedings of the Royal Society of London: Series B, Biological Sciences* 267:2327–2331.
- Hartline, D.K., Buskey, E.J., and Lenz, P.H. 1999. Rapid jumps and bioluminescence elicited by controlled hydrodynamic stimuli in a mesopelagic copepod, *Pleuromamma xiphias*. *Biological Bulletin* 197:132–143.
- Haury, L.R., Kenyon, D.E., and Brooks, J.R. 1980. Experimental evaluation of the avoidance reaction of *Calanus finmarchicus*. *Journal of Plankton Research* 2:187–202.
- Hernandez Molejon, O.G. and Alvarez-Lajonchere, L. 2003. Culture experiments with *Oithona oculata* Farran, 1913 (Copepoda: Cyclopoida), and its advantages as food for marine fish larvae. *Aquaculture* 219:471–483.
- Hinshaw, J.M. 1985. Effects of illumination and prey contrast on survival and growth of larval yellow perch *Perca flavescens*. *Transactions of the American Fisheries Society* 114:540–545.
- Holling, C.S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Canadian Entomologist* 91:293–320.
- Houde, E.D. 1973. Some recent advances and unsolved problems in the culture of marine fish larvae. *Proceedings of the World Mariculture Society* 3:83–112.
- Hunter, J.R. 1981. Feeding ecology and predation of marine fish larvae. In *Marine Fish Larvae: Morphology, Ecology and Relation to Fisheries*, edited by R. Lasker, pp. 33–77. Seattle, Washington, USA: University of Washington Press.
- Hwang, J.-S., Costello, J.H., and Strickler, J.R. 1994. Copepod grazing in turbulent flow: elevated foraging behavior and habituation of escape responses. *Journal of Plankton Research* 16:421–431.
- James, C.M. and Al-Khars, A.M. 1986. Studies on the production of planktonic copepods for aquaculture. *Syllogeus* 58:333–340.
- Janssen, J. 1981. Searching for zooplankton just outside Snell's window. *Limnology and Oceanography* 26:1168–1171.
- Janssen, J., Jones, W.R., Whang, A., and Oshel, P.E. 1995. Use of the lateral line in particulate feeding in the dark by juvenile alewife (*Alosa pseudoharengus*). *Canadian Journal of Fisheries and Aquatic Sciences* 52:358–363.
- Katona, S.K. 1973. Evidence for sex pheromones in planktonic copepods. *Limnology and Oceanography* 18:574–583.

- Kerfoot, W.C. 1982. A question of taste: crypsis and warning coloration in freshwater zooplankton communities. *Ecology* 63:538–554.
- Kjørboe, T. and Sabatini, M. 1994. Reproductive and life cycle strategies in egg-carrying cyclopoid and free-spawning copepods. *Journal of Plankton Research* 16:1353–1366.
- Kjørboe, T., Saiz, E., and Visser, A. 1999. Hydrodynamic signal perception in the copepod *Acartia tonsa*. *Marine Ecology Progress Series* 179:97–111.
- Kjørboe, T. and Visser, A. 1999. Predator and prey perception in copepods due to hydromechanical signals. *Marine Ecology Progress Series* 179:81–95.
- Kramer, D.L. and McLaughlin, R.L. 2001. The behavioral ecology of intermittent locomotion. *American Zoologist* 41:137–153.
- Kremer, P. 1979. Predation by the ctenophore *Mnemiopsis leidy* in Narragansett Bay, Rhode Island. *Estuaries* 2:97–105.
- Lasker, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. *Fishery Bulletin of the U.S. Department of Commerce* 73:453–462.
- Lauder, G.V. 1983. Prey capture hydrodynamics in fishes: experimental tests of two models. *Journal of Experimental Biology* 104:1–13.
- Leger, P., Bengtson, D.A., Simpson, K.L., and Sorgeloos, P. 1986. The use and nutritional value of *Artemia* as a food source. *Oceanography and Marine Biology: an Annual Review* 24:521–623.
- Lenz, P.H. and Hartline, D.K. 1999. Reaction times and force production during escape behavior of the calanoid copepod *Undinula vulgaris*. *Marine Biology* 133:249–258.
- Lenz, P.H., Hartline, D.K., and Davis, A. 2000. The need for speed. I. Fast reactions and myelinated axons in copepods. *Journal of Comparative Physiology A* 186:337–345.
- Lindquist, N. and Hay, M.E. 1996. Palatability and chemical defense of marine invertebrate larvae. *Ecological Monographs* 66:431–450.
- Lonsdale, D.J., Heinle, D.R., and Siegfried, C. 1979. Carnivorous feeding behavior of the adult calanoid copepod *Acartia tonsa* Dana. *Journal of Experimental Marine Biology and Ecology* 36:235–248.
- MacKenzie, B.R., Miller, T.J., Cyr, S., and Leggett, W.C. 1994. Evidence for a dome-shaped relationship between turbulence and larval fish ingestion rates. *Limnology and Oceanography* 39:1790–1799.
- Madin, L.P. 1988. Feeding behavior of tentaculate predators: *in situ* observations and a conceptual model. *Bulletin of Marine Science* 43:413–429.
- Marshall, S.M. 1973. Respiration and feeding in copepods. *Advances in Marine Biology* 11:57–120.
- Mauchline, J. 1998. The biology of calanoid copepods. *Advances in Marine Biology* 33:1–701.
- May, R.C. 1970. Feeding larval marine fishes in the laboratory: a review. *Reports of the California Cooperative Oceanic Fisheries Investigation* 14:76–83.
- McEvoy, L.A., Naess, T., Bell, J.G., and Lie, O. 1998. Lipid and fatty acid composition of normal and malpigmented Atlantic halibut (*Hippoglossus hippoglossus*) fed enriched *Artemia*: a comparison with fry fed wild copepods. *Aquaculture* 163:237–250.
- McMichel, R.H., Jr., and Peten, K.M. 1989. Early life history of spotted sea trout, *Cynoscion nebulosus* (Pisces: Sciaenidae) in Tampa Bay, Florida. *Estuaries* 12:98–110.
- Miller, T.J., Crowder, L.B., Rice, J.A., and Marschall, E.A. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Canadian Journal of Fisheries and Aquatic Sciences* 45:1657–1670.
- Millinski, M. 1977a. Experiments on the selection by predators against spatial oddity of their prey. *Zeitschrift für Tierpsychologie* 43:311–325.
- Millinski, M. 1977b. Do all members of a swarm suffer the same predation? *Zeitschrift für Tierpsychologie* 45:373–388.
- Miralto, A., Ianora, A., Poulet, S.A., Romano, G., and Laabir, M. 1996. Is fecundity modified by crowding in the copepod *Centropages typicus*? *Journal of Plankton Research* 18:1033–1040.
- Montgomery, J.C. 1989. Lateral line detection of planktonic prey. In *The Mechanosensory Lateral Line: Neurobiology and Evolution*, edited by S. Coombs, P. Gorner, and H. Munz, pp. 561–574. New York, New York, USA: Springer-Verlag.
- Montgomery, J.C. and Saunders, A.J. 1985. Functional-morphology of the piper *Hyporhamphus ihi* with reference to the role of the lateral line in feeding. *Proceedings of the Royal Society of London: Series B, Biological Sciences* 224:197–208.
- Morgan, S.G. 1989. Adaptive significance of spination in estuarine crab zoeae. *Ecology* 70:464–482.
- Morgan, W.L. and D.A. Ritz. 1984. Effect of prey density and hunger state on capture of krill *Nyctiphanes australis* Sars, by Australian salmon, *Arripis trutta* (Block and Schneider). *Journal of Fish Biology* 24:51–58.
- Neill, S.R.S.J. and Cullen, J.M. 1974. Experiments on whether schooling by their prey affects the hunting behavior of cephalopod and fish predators. *Journal of Zoology* 172:549–569.

- Newbury, T.K. 1972. Vibration perception by chaetognaths. *Nature* 236:459–460.
- O'Connell, C.O. 1972. The interrelation of biting and filtering in the feeding activity of the northern anchovy (*Engraulis mordax*). *Journal of the Fisheries Research Board of Canada* 29:285–293.
- Ohguchi, O. 1978. Experiments on the selection against colour oddity of water fleas by three-spined sticklebacks. *Zeitschrift für Tierpsychologie* 47:254–267.
- Ohman, M.D. 1986. Predator-limited population growth of the copepod *Pseudocalanus* sp. *Journal of Plankton Research* 8:673–713.
- Ohman, M.D. 1988. Behavioral responses of zooplankton to predation. *Bulletin of Marine Science* 43:530–550.
- Ohno, A., Takahashi, T., and Yashuhiko, T. 1990. Dynamics of exploited populations of the calanoid copepod *Acartia tsuensis*. *Aquaculture* 84:27–39.
- Pennington, J.T. and Chia, F. 1984. Morphological and behavioral defenses of trochophore larvae of *Sabellaria cementarium* (polychaeta) against four planktonic predators. *Biological Bulletin* 167:168–175.
- Purcell, J.E. 1992. Effects of predation by the scyphomedusan *Chrysaora quinquecirrha* on zooplankton populations in Chesapeake Bay. *Marine Ecology Progress Series* 87:65–76.
- Reid, J.W., Hamilton, R., IV, and Duffield, R.M. 2002. First confirmed New World record of *Apocyclops dengizicus* (Lepeshkin), with a key to the species of *Apocyclops* in North America and the Caribbean region (Copepoda: Cyclopidae). *Jeffersoniana* 10:1–25.
- Rothschild, B.J. and Osborn, T.R. 1988. Small-scale turbulence and plankton contact rates. *Journal of Plankton Research* 10:465–474.
- Salgado, S.D. and Hoyt, R.D. 1996. Early behavior formation in fathead minnow larvae, *Pimephales promelas*: implications for sensory function. *Marine and Freshwater Behaviour and Physiology* 28:91–106.
- Sekiguchi, H. 1974. Relation between ontogenetic vertical migration and mandibular gnathobase in pelagic copepods. *Bulletin of the Faculty of Fisheries Mie University* 1:1–10.
- Stemberger, R.S. and Gilbert, J.J. 1987. Multiple species induction of morphological defenses in the rotifer *Keratella testudo*. *Ecology* 68:370–378.
- Støttrup, J.G. and Norsker, N.H. 1997. Production and use of copepods in marine fish larviculture. *Aquaculture* 155:231–247.
- Strickler, J.R. 1975. Intra- and interspecific information flow among planktonic copepods: receptors. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 19:2951–2958.
- Sundby, S. 1997. Turbulence and ichthyoplankton: influence on vertical distribution and encounter rates. *Scientia Marina* 61:159–176.
- Sundby, S., Ellertsen, B., and Fossum, P. 1994. Encounter rates between first-feeding cod larvae and their prey during moderate to strong turbulent mixing. *ICES Marine Science Symposium* 198:393–405.
- Tollrian, R. 1995. Predator-induced morphological defenses: costs, life history shifts and maternal effects in *Daphnia pulex*. *Ecology* 76:1691–1705.
- Treisman, M. 1975. Predation and the evolution of gregariousness. I. Models for concealment and evasion. *Animal Behaviour* 23:779–800.
- Ueda, H., Kuwahara, A., Tanaka, M., and Azeta, M. 1983. Underwater observations on copepod swarms in temperate and subtropical waters. *Marine Ecology Progress Series* 11:165–171.
- Van Duren, L.A. and Videler, J.J. 1996. The trade-off between feeding, mate seeking and predator avoidance in copepods: behavioral responses to chemical cues. *Journal of Plankton Research* 18:805–818.
- Viitasalo, M., Kiørboe, T., Flinkman, J., Pederson, L., and Visser, A.W. 1998. Predation vulnerability of planktonic copepods: consequences of predator foraging strategies and prey sensory abilities. *Marine Ecology Progress Series* 175:129–142.
- Vine, I. 1973. Detection of prey flocks by predators. *Journal of Theoretical Biology* 40:207–210.
- Vinyard, G.L. and O'Brien, W.J. 1976. Effects of light and turbidity on the reactive distance of bluegill (*Lepomis macrochirus*). *Journal of the Fisheries Research Board of Canada* 33:2845–2849.
- Watanabe, T., Katajima, C., and Fujita, S. 1983. Nutritional value of live organisms used in Japan for mass propagation of fish: a review. *Aquaculture* 34:115–143.
- Williams, P.J., Brown, J.A., Gotceitas, V., and Pepin, P. 1996. Developmental changes in escape response performance of five species of marine larval fish. *Canadian Journal of Fisheries and Aquatic Sciences* 53:1246–1253.
- Witt, U., Quantz, G., Kuhlmann, O., and Kattner, G. 1984. Survival and growth of turbot larvae, *Scophthalmus maximus* L. reared on different food organisms with special regard to long-chain polyunsaturated fatty acids. *Aquacultural Engineering* 3:177–190.
- Wright, D.I. and O'Brien, W.J. 1982. Differential location of *Chaoborous* larvae and *Daphnia* by fish: the importance of motion and visible size. *American Midland Naturalist* 108:68–73.

- Yen, J. and Fields, D.M. 1992. Escape response of *Acartia hudsonica* (Copepoda) nauplii from the flow field of *Temora longicornis* (Copepoda). *Ergebnisse der Limnologie/Advances in Limnology. Stuttgart* 36:123–134.
- Yen, J., Lenz, P.H., Gassie, D.V., and Hartline, D.K. 1992. Mechanoreception in marine copepods: electrophysiological studies of the first antennae. *Journal of Plankton Research* 14:495–512.
- Yen, J. and Strickler, J.R. 1996. Advertisement and concealment in the plankton: what makes a copepod hydrodynamically conspicuous? *Invertebrate Biology* 115:191–205.
- Zaret, T.M. 1972. Predators, invisible prey, and the nature of polymorphism in the Cladocera (Class Crustacea). *Limnology and Oceanography* 17:171–184.
- Zaret, T.M. 1980. The effect of prey motion on planktivore choice. In *Evolution and Ecology of Zooplankton Communities*, edited by W.C. Kerfoot, pp. 599–603. Hanover, New Hampshire, USA: University Press of New England.
- Zaret, T.M. and Kerfoot, W.C. 1975. Fish predation on *Bosmina longirostris*: body size selection versus visibility selection. *Ecology* 56:232–237.