

BEHAVIORAL RESPONSES OF ZOOPLANKTON TO PREDATION

M. D. Ohman

ABSTRACT

Many behavioral traits of zooplankton reduce the probability of successful consumption by predators. Prey behavioral responses act at different points of a predation sequence, altering the probability of a predator's success at encounter, attack, capture or ingestion. Avoidance behavior (through spatial refuges, diel activity cycles, seasonal diapause, locomotory behavior) minimizes encounter rates with predators. Escape responses (through active motility, passive evasion, aggregation, bioluminescence) diminish rates of attack or successful capture. Defense responses (through chemical means, induced morphology) decrease the probability of successful ingestion by predators. Behavioral responses of individuals also alter the dynamics of populations. Future efforts to predict the growth of prey and predator populations will require greater attention to avoidance, escape and defense behavior. Prey activities such as occupation of spatial refuges, aggregation responses, or avoidance responses that vary according to the behavioral state of predators can alter the outcome of population interactions, introducing stability into prey-predator oscillations. In variable environments, variance in behavioral traits can "spread the risk" (den Boer, 1968) of local extinction. At present the extent of variability of prey and predator behavior, as well as the relative contributions of genotypic variance and of phenotypic plasticity, are not well known.

Charles Elton (1927) asserted the primacy of predation as a process regulating the abundance of natural populations, finding (p. 101) "... enemies ... more important than food-supply as a direct limiting check on numbers of most animals." Evidence for the importance of predation as a direct mechanism restricting the abundance, and composition, of zooplankton assemblages developed in subsequent decades (Hrbáček, 1962; Brooks and Dodson, 1965; Neill, 1975; Landry, 1976; Kerfoot, 1980; Zaret 1980a; Koslow, 1981; Harris et al., 1982; Ohman, 1986; Kerfoot and Sih, 1987). However, this session of the Zooplankton Behavior Symposium moved beyond the direct effects of predators as a limiting check on numerical abundance of zooplankton. It concerned the indirect effects (*sensu* Kerfoot and Sih 1987) of predators as agents of natural selection that shape the responses of planktonic prey. As identified by Miller and Kerfoot (1987), there are three classes of such indirect, or nonlethal, effects of predators: behavioral responses, chemical signals and effects mediated through a third species. The behavioral consequences are the focus of the present overview.

This overview will emphasize the behavioral adaptations of planktonic prey organisms rather than those of predators. Many aspects of predator activity (including sensory tuning, search image formation, locomotion, luring, selection/rejection and aggregation responses) are addressed in other sessions held at this symposium. Other sources for review may be found in Zaret (1980a), Kerfoot (1980), and Kerfoot and Sih (1987), as well as in specialized monographs. To some extent the boundary drawn between prey and predator behavior is artificial because of the possibility of coevolved responses, as discussed further below. Also, prey adaptations to predation that lie outside the realm of behavior are not addressed. These include permanent or invariable changes in morphological characters (e.g., body size [Havel, 1987]; spination [Gilbert, 1966; Kerfoot, 1975]; gelatinous sheaths [Stemberger and Gilbert, 1987]; tissue transparency [Kerfoot,

Table 1. Types of behavioral responses of zooplankton to predators and the component of a predation sequence that is affected

Prey response	Component affected
Avoidance	Encounter
Spatial refugia	
Diel rhythms	
Seasonal refugia	
Locomotor behavior	
Escape	Attack, capture
Motility	
Passive evasion	
Aggregation	
Bioluminescence	
Defense	Ingestion
Chemical	
Inducible morphology	

1982]; pigmentation [Zaret, 1980a] and life history traits [Dorazio and Lehman, 1983; Sih, 1987]), as contrasted with those induced by predators.

This contribution will use the components of predation framework of Holling (1966) that has been widely applied in the analysis of prey-predator interactions (Gerritsen and Strickler, 1977; Greene, 1983; O'Brien, 1987). Accordingly, a predation sequence is considered in its consecutive components: here considered as encounter, attack, capture and ingestion. Prey behavioral responses will be analyzed according to the step in the predation sequence where they reduce a predator's probability of success. This analysis builds upon, and extends, the presentations by Kerfoot et al. (1980), Sih (1987) and Stemberger and Gilbert (1987).

Table 1 lists the types of behavioral responses to predators summarized herein, including (1) avoidance responses, which minimize the probability of encounter with a predator, (2) escape responses, minimizing the probability of attack or capture, once encounter has occurred and (3) defenses, decreasing the probability of successful ingestion after capture. The examples presented below are treated as adaptively significant behavior, although two caveats should be borne in mind. First, predation may not be the sole selective factor that leads to a particular behavior. Second, some behavioral responses, like other traits, may be selectively neutral or may be constrained by phylogeny rather than adaptively significant (Gould and Lewontin, 1979; Sih, 1987).

This overview will also attempt to place behavioral studies in a broader context, illustrating the consequences of individual behavior for populations. In so doing I heartily endorse the case made elsewhere (Hassell and May, 1985; May, 1986) for building upwards from the behavior of individuals to the dynamics of populations.

PREY RESPONSES

Avoidance

Several types of avoidance behavior are employed by prey organisms to minimize encounters with predators (Table 1). These include: occupation of spatial refuges where predators are absent or rare; diel periodicity in feeding, spawning or molting activity such that times of day of peak predation risk are avoided;

seasonal diapause so as to enter a resting state in seasons of peak predator abundance or predator activity; and locomotory behavior that minimizes the rate of encounter with predators.

Spatial Refugia.—Prey can avoid encounters with predators by utilizing spatially different habitats, either during specific times of day or on a continuous basis. If predator feeding activity is restricted to a particular region of the water column and a specific time of day or night, diel vertical migration can reduce spatial overlap with predators. For visually conspicuous prey, diurnal descent to deep strata provides a daytime refuge from visually hunting planktivorous fish (Zaret and Suffern, 1976; Stich and Lampert, 1981; Gliwicz, 1986). However, other prey taxa may be more susceptible to predatory zooplankton, many of which hunt nocturnally (Federenko, 1975; Feigenbaum and Maris, 1984; Yen, 1985; Ohman, 1986). For the latter, reverse diel vertical migration—nocturnal descent to deep strata—provides a nighttime refuge from nonvisually hunting predators (Hairston, 1980; Ohman et al., 1983; Bayly, 1986). More complete discussion of diel vertical migration behavior can be found in the session of this symposium devoted to diel, seasonal and long-term patterns.

In addition to refugia attained on a daily basis through diel vertical migration, prey may attain a spatial refuge by permanent or transitory occupation of habitats unsuitable for predators. The littoral zone of some lakes may provide a refuge from some predators (Kerfoot, 1975). In open water areas, permanent occupation of depth strata different from those occupied by predators may occur, provided predators do not alter their vertical distribution in response to that of the prey.

Diel Rhythms.—Diel rhythms in prey behavior alter the probability of detection by predators. These diel activity patterns may be independent of migration behavior that modifies spatial distributions.

Diel periodicity in zooplankton feeding behavior, independent of vertical migration, has been documented for many organisms (Duval and Geen, 1976; Mackas and Bohrer, 1976; Yen, 1982; Nicolajsen et al., 1983; Feigenbaum and Maris, 1984; Head et al., 1985; Stearns, 1986; Head, 1986). Two consequences follow for the detection of prey by predators. First, planktonic animals with full guts can be more conspicuous visually than those with empty guts. Hence, nocturnally phased feeding may reduce the probability of detection by visually hunting predators. Second, in many zooplankters feeding and swimming are correlated activities (Gauld, 1966; Alldredge and Madin, 1982; Cowles and Strickler, 1983). Thus, diurnal reductions in feeding activity can also alter velocities and patterns of locomotion, diminishing encounter rates with predators (Gerritsen and Strickler, 1977).

Spawning activity of some copepod species occurs principally nocturnally (Marshall and Orr, 1955; Runge, 1985; Marcus, 1985). Egg release during darkness reduces the exposure of gravid females to visual predators, provided it is accompanied by migration to deeper waters by day.

Molting by crustacean zooplankton may also be nocturnally synchronized (Miller et al., 1984a). During ecdysis a protracted period may be required to shed the old exoskeleton, during which time a copepod may have reduced escape capabilities (Miller et al., 1984a) and diminished structural defense, due to the pliant texture of the newly forming exoskeleton. An individual may also be more conspicuous to visually hunting predators due to the enlarged visual outline of the molt plus body (pers. obs.). Hence, by confining molting activity to nocturnal hours, encounter frequencies with predators will be reduced during intervals of peak susceptibility to visual predators.

Seasonal Refugia. — In both marine and freshwater environments, fluctuations in the abundance of predators often have a strong seasonal component (Hutchinson, 1967; Kremer and Nixon, 1976; Ohman, 1986). Strickler and Twombly (1975) and Hairston (1987) have suggested that the seasonal diapause response exhibited by many zooplankters may be a means to avoid encounter with predators at times of high predation risk. Although environmental cues such as photoperiod or photoperiod-temperature interactions (Marcus, 1982) may be the proximate stimulus controlling the timing of diapause, one of its adaptive advantages may be predator avoidance.

Diapause is characterized by a suspension of growth and development. It has been observed in developmental stages ranging from eggs to adults (Grice and Marcus, 1981; Marcus, 1982). Diapause is usually accompanied by sinking to deeper waters in oceanic environments (Miller et al., 1984b; Ohman, 1987) or to sediments in shallow water environments (Grice and Marcus, 1981; Hairston, 1987). By sinking out of the surface layer, mortality due to planktonic predators can be reduced. Hairston and Walton (1986) suggest that the production of benthic resting eggs by the copepod *Diaptomus sanguineus* is appropriately timed to minimize seasonal predation by planktivorous sunfish. The results of a natural experiment were also consistent with this hypothesis. When a drought eliminated sunfish from a shallow pond but not a deeper pond, the timing of resting egg production shifted later in the year only in the shallow, fishless pond (Hairston and Walton, 1986).

Although deeper waters may have lower predator abundances than surface waters, they are not entirely risk-free environments. Alldredge et al. (1984) suggest that deep diapausing *Calanus pacificus* occurring in high densities may attract planktivorous fish. Also, because of the presence of deposit-feeding benthic organisms, sediments are not without hazards to resting stages of planktonic organisms. However, the risks of benthic predation are not readily predictable without appropriate experiments. For example, Marcus (1984b) illustrated that copepod diapause eggs residing in sediments can survive passage through the gut of deposit-feeding polychaetes. Strathmann (1982) compared the relative risks of pelagic and benthic predation for marine invertebrates. Further comparisons of mortality rates in surface vs. deep water (or benthic) environments will help identify those environments in which diapause does indeed confer a reduction in mortality.

Locomotory Behavior. — For prey co-occurring in the same parcel of water with predators, prey locomotory activity can alter encounter frequencies and the efficiency of detection by predators. Gerritsen and Strickler (1977) developed an encounter model for randomly dispersed, randomly oriented predators searching for prey in three dimensions. Encounter rates were found to depend strongly on the relative rates of motion of prey and predator and on the encounter radius of the predator. Two classes of predators were identified from their model: stationary, or ambush predators which most efficiently utilize fast moving prey and cruising predators which most efficiently utilize slow moving prey (Gerritsen and Strickler, 1977). The dichotomy arises from considerations of energetic efficiency. Predators will encounter fast moving prey, at lowest energetic cost, by remaining stationary. Predators must move to encounter slow moving prey, but their efficiency declines at very high swimming speeds.

Gerritsen (1984) extended this encounter model to three different sizes of predators. Consideration of the power requirements for cruising, determined by different drag characteristics for Protozoa (Reynolds number [Re] < 0.1), macro-

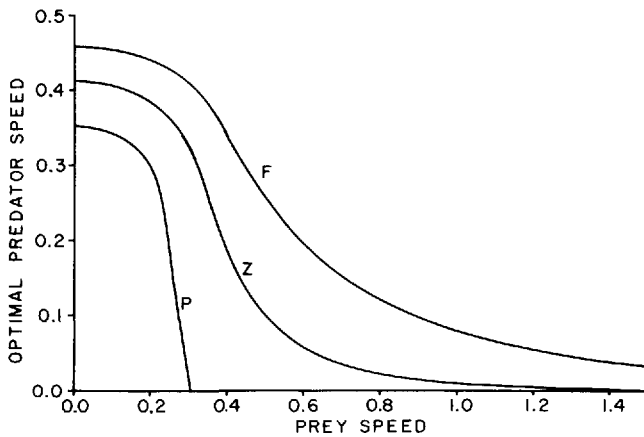


Figure 1. Optimal predator swimming speed as a function of prey speed, as predicted by the foraging model of Gerritsen (1984). The energy costs for swimming vary for three classes of predators swimming in different Reynolds number regimes: P = protozoa ($Re < 0.1$), Z = zooplankton ($0.1 < Re < 100$) and F = fish ("high" Re). Time is nondimensional.

zooplankton ($0.1 \leq Re \leq 100$) and fish (high Re), confirmed the existence of the two optimal types of predator swimming. Figure 1 (from Gerritsen, 1984) illustrates that as prey speed increases, the transition from cruising to ambush behaviors for predatory Protozoa is quite abrupt. The transition for predatory zooplankton and planktivorous fish is somewhat more gradual but delineates the major ambush/cruising division. Greene (1985) extended this dichotomy to better reflect the morphological and behavioral diversity of predatory marine zooplankton, some of which fed by raptorial means and some by entangling their prey.

Hence, the prey swimming speed that best avoids encounters with predators depends on the predominant type of predator present. Confronted with cruising predators, a prey organism should swim at moderate speeds. Confronted with ambush predators, a prey organism should decrease its speed to near zero, subject to the constraint that motion is necessary to find food and mates (Gerritsen and Strickler, 1977).

The pattern of swimming activity, in addition to speed of motion, can affect the probability of encounter with or detection by a predator. For visual predators, prey motion can alter detectability and the magnitude of predator response (Zaret, 1980b; O'Brien, 1987). For nonvisual predators, including most species of predatory zooplankton, patterns of prey motion can alter the strength of hydrodynamic, tactile or chemical cues detected by predators. For example, Kirk (1985) contrasted the flow signals generated by the cladoceran *Daphnia pulex* and the copepod *Diaptomus hesperus* as they swam past a hot-wire anemometer probe. The cladoceran and copepod flow signals differed in several regards, including overall temporal pattern, accelerations and presence of an oscillatory component of the flow. All of these components of prey motion can be important for mechanoreceptors of predators.

Within the Copepoda alone considerable differences exist among species in swimming behavior, appendage motions and rhythmic activity. Gauld (1966) described, from visual observations, differences in swimming and feeding activity of several copepod species. Interspecific differences in appendage motions, activity/rest intervals and associated fluid flow have now been identified and quantified by techniques of high-speed cinematography (Strickler, 1982; Price and Paffen-

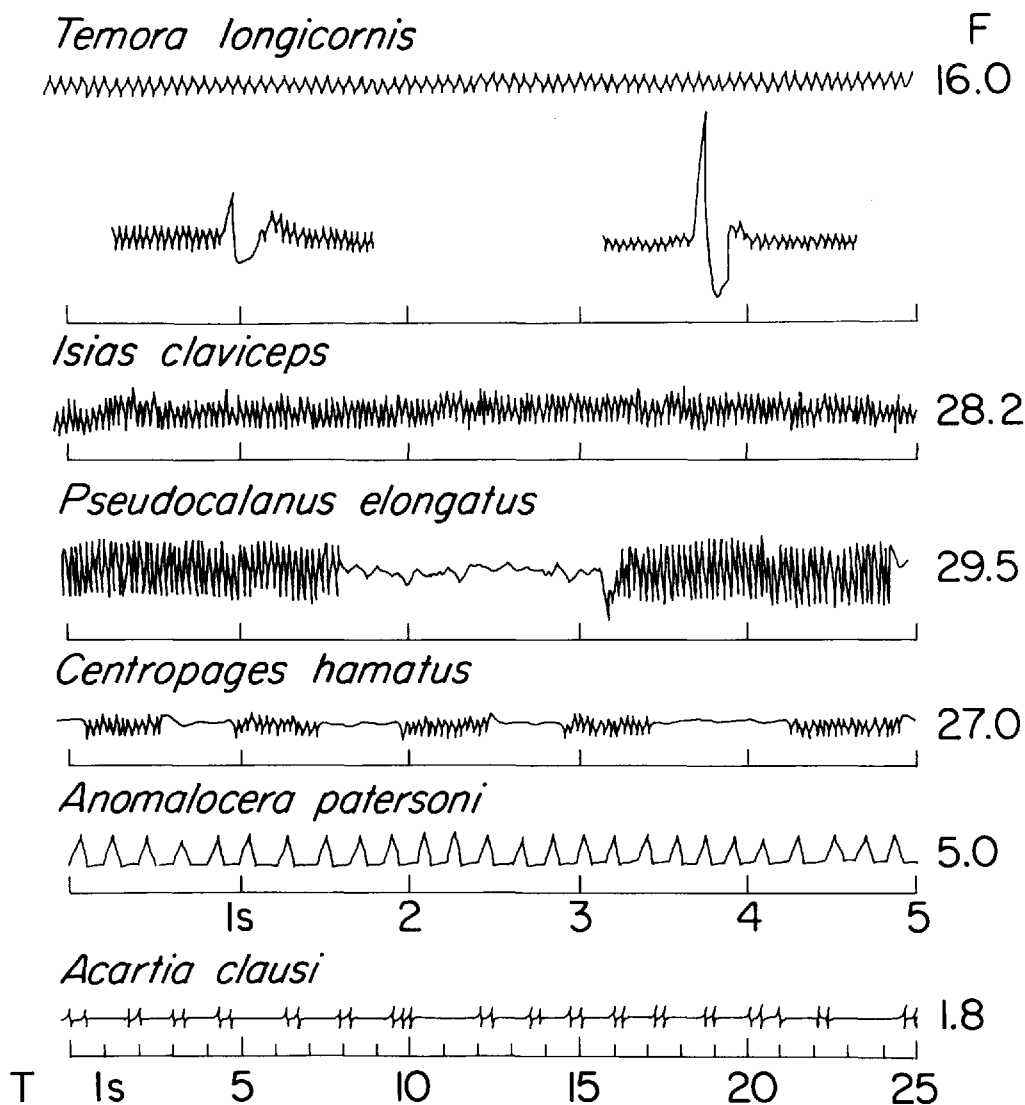


Figure 2. Impedance pneumograph recordings of motions of the second antennae of six species of calanoid copepods. In the second line of recordings *Temora longicornis* was disturbed by a change in flow direction and exhibited escape responses. T indicates time marks at 1 s intervals and F indicates the A2 beat frequency in Hz. Note the different time scale for *Acartia*. Redrawn from Gill (1987) with permission.

höfer, 1985) and video recording (Cowles and Strickler, 1983; Buskey and Swift, 1985). Recently Gill (1987) compared the motion of the second antennae (A2) of 6 species of calanoid copepods from impedance pneumograph recordings. Figure 2 (from Gill, 1987) illustrates the considerable variability among species in patterns of motion of the same appendage. For example, contrast the smooth, continuous A2 beats of *Temora* and *Isias* with the activity/rest cycle of *Pseudocalanus* and *Centropages* and the jerky low-frequency motions of *Anomalocera* and *Acartia*. If rhythmic patterns of motion are important to predators (Feigenbaum and

Reeve, 1977), it might be hypothesized that such motions could be a behavioral means for prey to alter encounter and detection probabilities.

Escape

Following encounter with predators a variety of escape behaviors are employed to elude capture (Table 1). Escape behaviors described below include prey motility, passive evasion, aggregation responses and bioluminescence.

For many species the ability to evade successful capture by predators varies with size and developmental stage, leading to a pattern of risk varying with size or stage. Pastorok (1981) defined a "vulnerability" function that makes use of two general relationships between a predator (nonvisually hunting, in his case) and the size of its prey. First, encounter rates tend to increase with prey size (as a consequence of increased swimming speed) and second, predator capture success decreases with prey size (as a consequence of prey escape behavior). The product of this encounter rate curve and this capture success curve gives a dome shaped, concave downward "vulnerability" function. Pastorok (1981) found that differential vulnerability of prey as predicted by this function, rather than active behavioral choice or optimal foraging behavior by the predator, accounted for the apparent size selection of prey by larval *Chaoborus*.

The vulnerability function approach has also been applied in a comparative study of predation by ctenophores, chaetognaths and predatory copepods on a common prey (Greene and Landry, 1985; Greene, 1986). The study is unique in its comparison of predation by both ambush and cruising predators on all post-embryonic stages of the calanoid copepod *Calanus pacificus*. Considerable differences remain between the stage-specific patterns of vulnerability of *Calanus* detected in the laboratory (Greene, 1986) and the stage-specific mortality observed in nature (Mullin and Brooks, 1970), but the approach appears promising. Such studies confirm that escape behaviors that vary with developmental stage (as well as encounter rates) must be understood to predict predation patterns in the plankton.

Motility.—Zooplankton species differ in their ability to evade suction pipets in the laboratory as well as plankton nets (Fleminger and Clutter, 1965; Brinton and Townsend, 1981; Wiebe et al., 1982), plankton pumps (Miller and Judkins, 1981), divers (Hamner and Carleton, 1979) and submersibles (Mackie, 1985) in the field. Active evasion behavior can dramatically alter the probability of capture by predators as well as by sampling devices. Many planktivorous fish species capture prey by the suction established by the buccal siphon (Drenner et al., 1978; O'Brien, 1987). Predatory copepods, in turn, may establish feeding currents that entrain prey (Landry, 1978). The ability of prey taxa to respond to local fluid deformations associated with predator feeding and locomotion is thus important to the successful evasion of capture.

Singarajah (1969; 1975) documented differential escape abilities of several species of copepods and larval stages of other invertebrates. Landry (1978) demonstrated that copepod escape ability varies with size and developmental stage. Figure 3 (from Landry, 1978) illustrates that the efficiency with which a siphon current captured different developmental stages decreased monotonically between early naupliar and early copepodid stages. This trend corresponds to an increasingly strong escape response with increasing size and with the addition of swimming legs at the metamorphosis from nauplius VI to copepodid I. Escape responses by nauplii and other potential prey reduce rates of successful capture by adult *Diaptomus pallidus* (Williamson and Vanderploeg, 1988)

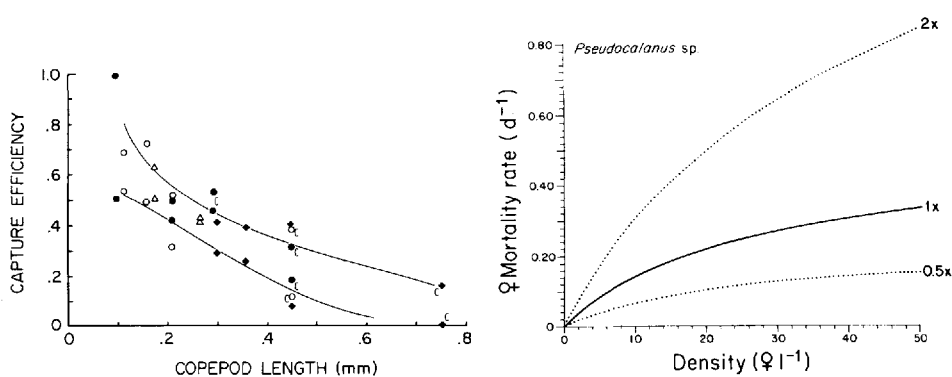


Figure 3. (Left) Efficiency of capture of different developmental stages of copepods by a siphon current, as a function of copepod length. Prey identities are: *Acartia tonsa* (O), *Paracalanus parvus* (●), *Labidocera trispinosa* (Δ) and *Calanus pacificus* (+). Experiments were performed at two current speeds, the lower data points and line reflecting half the speed of the upper. Reprinted from Landry (1978) with permission.

Figure 4. (Right) Dependence of the instantaneous mortality rate of the copepod *Pseudocalanus* sp. (due to consumption by predators) on the population density of *Pseudocalanus* sp. The three curves show mortality for the density of predators measured in Dabob Bay (1x), for twice the measured predator densities (2x) and for half the measured densities (0.5x). Five hundred *Pseudocalanus* sp. contained within 1 m³ were assumed to cluster in localized patches; prey densities could thus vary from 0.5 to 50 liter⁻¹. Reprinted from Ohman (1986) with permission.

Haury et al. (1980) analyzed the properties of fluid flow that elicit an escape response by *Calanus finmarchicus*. They concluded that the amount and the rate of fluid deformation were the principal sources of flow stimuli for this copepod. Fluid accelerations and fluid pressure were concluded to be of little importance as stimuli inducing escape responses. Fluid vibrations (near-field displacement) act over too short a distance to account for the reaction distances documented by Haury et al. (1980), but this stimulus was thought by Schröder (1960) to be of importance for *Mixodiaptomus laciniatus*. Kirk and Gilbert (1988) illustrate that simple, steady flows elicit escape responses of the rotifer *Polyarthra remata*.

Differential escape responses of cladocerans, cyclopoid and calanoid copepods account for the apparent prey selectivity of filter-feeding gizzard shad (Drenner and McComas, 1980). Calanoid copepods, with best developed escape responses, were ingested by shad at the lowest rates. Predation by filter-feeding gizzard shad shifts the composition of the zooplankton assemblage to the largest, most evasive prey (Drenner et al., 1982) rather than to the smallest prey as predicted by earlier size selective predation arguments (Brooks and Dodson, 1965).

Yen's comprehensive study of predation by the copepod *Euchaeta elongata* on developmental stages of *Calanus pacificus* and adults of other copepods revealed peak capture rates on intermediate-sized prey (Yen, 1985). Yen attributed this pattern to escape responses of the late copepodid stages of *Calanus pacificus* and difficulty for *Euchaeta* in detecting or handling youngest developmental stages of *Calanus*.

Euphausiids and mysids, among the fastest swimming zooplankters, exhibit excellent escape abilities. They can respond to hydrodynamic disturbances (Mauchline, 1980; Bowers, 1988) and to visual stimuli (Land, 1980; Brinton and Townsend, 1980; Wiebe et al., 1982). Even nets with mouth openings of 10 m² moving at 100 cm s⁻¹ may undersample some euphausiid species (Wiebe et al.,

1982). The antarctic krill, *Euphausia superba*, may not be efficiently captured by any invasive sampling procedure used by the scientific community (Brinton et al., 1987). Hamner et al. (1983) reported an unusual escape response by a swarm of antarctic krill. Following disturbance by divers, Hammer et al. suggested that krill molted spontaneously and escaped, leaving behind exoskeletons suspended in the water column.

Rotifers exhibit active escape responses, among other escape and defense behaviors (Stemberger and Gilbert, 1987; Walton, 1988). After physical contact with a predator, *Polyarthra vulgaris* may initiate an escape within as little as 7 milliseconds (Gilbert, 1985). Williamson (1987) documented the importance of active escape responses for rotifers encountering suspension feeding copepods (*Diaptomus pallidus*). Differences among seven rotifer species in behavior, spination and lorica roughness accounted for differential susceptibility to predation. Two rotifer species which have movable appendages used in escape (and in confounding capture, in the case of *Filinia terminalis*) had very low probabilities of capture (0.03 for *Polyarthra major* and 0.06 for *Filinia terminalis*). In those few encounters where copepods did succeed in capturing these two species, they were ingested with a probability of 1.0, confirming the importance of pre-capture evasion.

Pelagic cnidarians and ctenophores, usually obligate carnivores, are themselves prey for a variety of organisms. Among their predators are other coelenterates and fish. When the siphonophore *Nanomia cara* comes into contact with any resistant object or with the air-water interface, a concerted thrust can propel the colony 10–15 cm in the opposite direction (Mackie, 1964). The hydrozoan *Aglantha digitale*, which also swims by pulsatile jet propulsion, exhibits both slow swimming and fast swimming activity (Donaldson et al., 1980). Fast swimming is an escape response elicited by tactile contact or a pressure wave (Donaldson et al., 1980). It consists of one to three violent contractions and is accompanied by retraction of tentacles, presumably to reduce hydrodynamic drag during escape (Donaldson et al., 1980; Roberts and Mackie, 1980).

Numerous other examples could be cited. The occurrence of active escape responses is widespread among zooplankton confronted with either the tactile, hydrodynamic, chemical or visual stimuli that suggest the presence of a predator.

Passive Evasion. — In contrast to active swimming as a means to escape predators, passive sinking responses, reductions in activity or other means of passive evasion can dramatically reduce the ability of predators to locate their prey. When the thecosomatous pteropod *Limacina* (= *Spiratella*) *helicina* is attacked by its gymnosomatous predator it may cease wing movements and sink through the water column (Lalli, 1970). Kerfoot et al. (1980) argue that most cladoceran species lack the ability for the rapid, accelerating escape responses used by copepods, hence cladocerans must use other adaptations for evading capture or ingestion. Among these is akinesis or a “dead man” response such as that exhibited by *Bosmina longirostris* when attacked by the predatory cyclopoid *Cyclops* (Kerfoot, 1978). After contact with *Cyclops*, *Bosmina* is able to evade subsequent detection and capture by withdrawing its antennae into lateral sheaths, tightly apposing the halves of the carapace and sinking slowly. The ability of a predator to relocate and capture prey may be greatly diminished by passive sinking responses and reductions in hydrodynamic disturbances.

The predatory copepod *Euchaeta elongata* is less able to capture passive, heat-killed nauplii (Yen, 1985) and adult copepods (Yen, 1982) than their actively swimming, living counterparts. *Euchaeta* apparently requires the stimulus of prey swimming disturbances for detection. *Euchaeta* also does not ingest quiescent,

nonmoving eggs but does attack swimming fish larvae (Bailey and Yen, 1983). Prey may lower feeding rates in the presence of predators (Wong, 1988) or competitors (Folt and Goldman, 1981), possibly generating diminished hydrodynamic disturbances as a consequence. Some rotifers also employ passive escape behavior. When contacted by a predator or a large cladoceran many species retract their corona and sink in a hydrodynamically quiet manner (Stemberger and Gilbert, 1987). In another form of passive evasion, mayflies and stoneflies may "drift" downstream to escape predators (Peckarsky, 1982).

Aggregation.—Swarms, schools and shoals of several zooplankton taxa have been observed in diverse pelagic environments (Hardy, 1936; Hutchinson, 1967; Haury et al., 1978; Omori and Hamner, 1982; Zeldis and Jillett, 1982). Folt (1987) and Omori and Hamner (1982) summarize some of the benefits and costs of aggregation to planktonic animals. Among the adaptive advantages of aggregation behavior are the dilution of individual predation risk, confounding of predator search image in mixed species groups and increased probability of mate location. Among the disadvantages are depressed feeding rates or feeding efficiencies because of interference from conspecifics or from other taxa (Folt and Goldman, 1981; Folt, 1987; Wong, 1988), and the possibility that predation risk increases if patches attract predators (Folt, 1987). Hence, under some circumstances, aggregation may confer an escape for an individual through reduced probability of attack. Further studies that evaluate both costs and benefits of aggregation behavior (Folt, 1987) in dynamic patches are needed.

Bioluminescence.—Escapes can also be accomplished by dazzling or confusing predators with bioluminescent displays. Protean bioluminescence of dinoflagellates reduces their ingestion by copepods relative to conspecific, non-luminescent clones (Esaias and Curl, 1972; White, 1979; Buskey et al., 1983). Buskey and Swift (1985) reported that copepods and some other zooplankton taxa respond to simulated bioluminescent flashes by increasing mean swimming speed, number of rapid swimming bursts, rate of turning and distance travelled. Buskey and Swift (1985) also observed that a bioluminescent copepod species (*Metridia longa*) was more responsive to simulated copepod bioluminescence than was a non-luminescent species (*Calanus finmarchicus*), suggesting that flashes are also a form of intraspecific communication. As with aggregation behavior, a number of adaptive advantages have been proposed for bioluminescence (Herring, 1978; Porter and Porter, 1979; Young, 1983).

Defense

If capture has not been successfully eluded, post-capture defense mechanisms are invoked by some prey organisms (Table 1). These defenses increase the difficulty of handling or ingesting prey.

Chemical Defenses.—Secondary compounds that are noxious to predators and deter ingestion (or capture) have been documented in a number of organisms. In some instances the secretion or dispersal of defensive compounds is a behavioral response stimulated by encounter with predators. In other instances release is a continuous process, or compounds reside permanently within the organisms and prey rely on warning coloration to deter predators.

Some dinoflagellate species deter predation by copepods by allelopathy. Sykes and Huntley (1987) document the post-capture regurgitation of toxic dinoflagellates by *Calanus pacificus*. *Calanus* also lost motor control, exhibited elevated

heart rate and showed other acute responses to ingestion of some dinoflagellate species. Five of 13 dinoflagellate species investigated by Huntley et al. (1986) elicited particle rejection behavior by *Calanus*, confirming that the distribution of noxious compounds in dinoflagellates is species-specific. Since dinoflagellate toxicity can slow developmental rates of *Calanus* nauplii prior to the onset of feeding stages, extracellular release may be involved in dinoflagellate toxicity (Huntley et al., 1987).

Aquatic insects and water mites bear toxic compounds that deter fish predation (Kerfoot, 1982; Scrimshaw and Kerfoot, 1987). Scrimshaw and Kerfoot report that approximately 80 compounds have been identified from 68 species of aquatic arthropods. Dytiscid beetles, for example, release the contents of both prothoracic and pygidial bladders upon capture by fish, followed by immediate rejection and buccal flushing by the fish. The contents of the metathoracic glands in bugs may have several functions, including action as sexual attractants and alarm substances as well as defense mechanisms (Scrimshaw and Kerfoot, 1987).

Inducible Morphology.—Some morphological structures that serve as defenses to frustrate prey handling by predators are inducible. Hence, as contrasted with permanent invariable structures that may serve as defense mechanisms but are not altered in response to environmental stimuli, inducible defenses may be considered appropriate for the current review.

Developmental polymorphisms induced by predators occur within several planktonic taxa, including protozoans, rotifers and cladocerans (reviewed in Havel, 1987). The cases summarized by Havel include only freshwater taxa, but it is not clear whether it is the phenomenon or the distribution of research effort that is confined to freshwater organisms. It is commonly assumed that induced structures carry a cost in fitness, else they would be maintained permanently (Havel, 1987; Stemberger and Gilbert, 1987), but identification of the fitness costs of the induced defenses has proven difficult (Gilbert, 1980).

Stemberger and Gilbert (1987) list seven species of rotifers known to exhibit altered morphology in response to soluble factors released by predators. The predators include predatory rotifers (*Asplanchna*), cyclopoid copepods (*Mesocyclops*, *Tropocyclops*), calanoid copepods (*Epischura*) and cladocerans (*Daphnia*; Stemberger and Gilbert, 1987). In the presence of soluble factors released by these predators, rotifer spines may be lengthened or developed de novo or body size may increase. In contrast, tactile contact may mediate other responses of rotifers. Contact with predators causes some soft-bodied rotifers to retract the corona, causing bodies to swell and become turgid. Body turgor increases the difficulty to predators of grasping and ingesting their prey (Stemberger and Gilbert, 1987).

Among cladocerans, species of *Bosmina* and *Daphnia* alter mucro length, body size, helmets and crests in response to morphogens released by predatory copepods (*Epischura* spp.), insect larvae (notonectids and chaoborids) and adult *Anisops calcaratus* (Havel, 1987). Elaboration of such structures is associated with reductions in mortality. In response to a soluble morphogen released from predatory ciliates, several species of the ciliate *Euplotes* elaborate lateral wings and ridges that deter their predators (Kuhlmann and Heckmann, 1985).

FROM BEHAVIOR TO POPULATION DYNAMICS

The study of organismal behavior is of intrinsic interest, but the behavior of individuals also has important consequences for the dynamics of populations. Avoidance, escape and defense responses can alter population trajectories through time. This section will briefly illustrate the importance of building upwards from

the short term behavior of individuals to longer term population level responses of prey and predators. An important precedent can be found in the contribution of Hassell and May (1985), from which the title of this subsection is derived.

Most of the preceding section addresses behavioral adaptations of prey that alter the functional response of predators. Holling (1959; 1966) identified both the functional and numerical responses as key components of the interaction of prey and predator, and it is now apparent that the developmental and aggregative responses must be considered as well (Murdoch and Bence, 1987). Concerning the functional response, it is widely appreciated that foraging behavior can stabilize (or destabilize) prey-predator oscillations in planktonic ecosystems. Sigmoidal or Holling type III functional responses can lead to stable coexistence of prey and predator populations (Holling, 1959; Hassell, 1978; Ohman, 1984). "Switching" responses by generalist predators can also stabilize prey populations (Murdoch and Oaten, 1975; Landry, 1981). Prey behavior that modifies these predator functional responses will therefore affect population fluctuations. Developmental and numerical responses of predators can also be modified by prey behavior. The results of Williamson and Magnien (1982) imply that avoidance responses such as diel vertical migration behavior can alter both the growth rate and numerical abundance of predators.

Aggregation responses also alter population growth of prey and predators. Steele and Henderson (1981) noted pronounced variations in prey and predator abundance within field enclosures, in contrast to the more damped variations observed outside enclosures. Steele and Henderson concluded that the absence of random variation in predator abundance within field enclosures accounted for this difference; aggregation of planktonic predators damp fluctuations in prey abundance.

An example of the interactive effects of prey aggregation with predator aggregation is illustrated in Figure 4 (from Ohman, 1986). Ohman's sensitivity analysis assessed the variation in mortality rate that would accompany different levels of prey aggregation. Localized concentrations of the copepod *Pseudocalanus* sp. were permitted to vary from $0.5 \cdot \text{liter}^{-1}$ (even dispersion) to $50 \cdot \text{liter}^{-1}$ (aggregation) within a cubic meter of water. From knowledge of the functional response of the predators of *Pseudocalanus*, estimates of mortality were made, as indicated by the central line ($1 \times$) in Figure 4. At the lower range of prey concentrations, a doubling of prey density caused by aggregation behavior results in nearly a doubling of mortality rate. If predators are permitted to aggregate in addition to prey, ranging from $0.5 \times$ to $2 \times$ the average measured density of predators, substantial further variation in mortality rates can occur (Fig. 4). This analysis does not incorporate predator confusion or other possible density-dependent changes in feeding behavior (Folt, 1987). However, it underscores the need for better understanding of fine-scale prey dispersion patterns and the behavior that generates them, if the impact of predators on natural populations is to be predicted.

To capture the essential features of prey-predator dynamics, population dynamic models will need to incorporate the interaction of prey behavior with the functional, developmental, numerical and aggregative responses of predators.

Variability of Behavioral Traits.—In studies of zooplankton behavior conducted in the ocean, lakes and the laboratory, within-population variability in behavioral response is commonly considered unwanted noise masking a "dominant" behavioral signal. However, variability in behavior may contribute to adaptive genetic changes and is therefore an important subject of study. As stated by Vermeij (1982; also quoted in Sih, 1985): "If individuals do not vary with respect to the likelihood of being detected, pursued, or subdued by predators, selection

is impossible. . . .” This symposium sought, in part, to address how natural selection influences behavior. The generation and maintenance of variation in traits is a key component of this evolutionary process.

den Boer (1968) advanced the concept of “spreading of risk” such that a population persists longer, with lowered risk of extinction, when variability of traits occurs within the population. In an environmental mosaic where local variations exist in physical conditions, food concentration and predators, the probabilities of surviving and reproducing differ in different locales. Different traits may be selected for in different local environments or subpopulations. If a range of traits occurs within a population (i.e., summed over a number of subpopulations), that population is more likely to survive extreme conditions than is one with a single expression of a trait. For example, den Boer (1981) sampled two beetle species for 19 years and documented differences between them in the coherence of fluctuations of subpopulations. The species with unequally fluctuating subpopulations had an expected survival time about 10 times that of the species with subpopulations all fluctuating in parallel. (This result occurs entirely as a consequence of individual selection; for example, by means of a balanced polymorphism.)

The pelagic domains of oceans and large lakes can be heterogeneous environments, confronting planktonic organisms with the kind of environmental mosaic described by den Boer. Different patches of zooplankton within the same interbreeding population may encounter pronounced differences in thermal regime, food supply, predatory zooplankton and planktivorous fish. Further, a single “patch” may experience changes through time, as, for example, zooplankton entrained in cold core rings is transported from the continental slope to the oligotrophic Sargasso Sea (Wiebe et al., 1976) or a warm core ring’s fauna is transported from the Sargasso Sea to a continental slope environment (Cowles et al., 1987). Behavioral traits would be expected to vary in response to environmental change, rather than a single “optimal” behavior prevailing in all circumstances.

Genotypic vs. Phenotypic Solutions. — The extent to which variations in behavioral traits reflect phenotypic plasticity of individuals or genotypic polymorphisms within a population is not clear (Dingle, 1984; Runge and Myers, 1986). Further attention is needed to the distribution of genetic variability in behavioral traits in planktonic populations and the trade offs between genotypic and phenotypic variance (Ohman, 1983; Sih, 1987).

A few instances of genotypic variance in zooplankton behavior have been well documented. Weider (1984) identified clonal differences in diel vertical migration behavior of *Daphnia pulex* co-occurring within a single pond. Two clones, identified by allozyme markers, differed in both vertical and horizontal distribution. One clone predominated in shallow strata while a separate clone predominated in deeper strata (Weider, 1984). Clones differed in fitness-related life history traits and varied in relative abundance as conditions changed in the pond (Weider, 1985).

Marcus (1984a) identified geographic differentiation in the diapause response of the pontellid copepod *Labidocera aestiva*. Low latitude populations rarely enter diapause. Bucklin and Marcus (1985) found significant genetic differentiation, as inferred from allozyme variation, of populations of *L. aestiva* over the same geographic scale. Allozyme frequencies of euphausiids collected in the open western North Atlantic fluctuated over time (Bucklin and Wiebe, 1986), though these variations apparently occurred in a random manner (Bucklin, 1986).

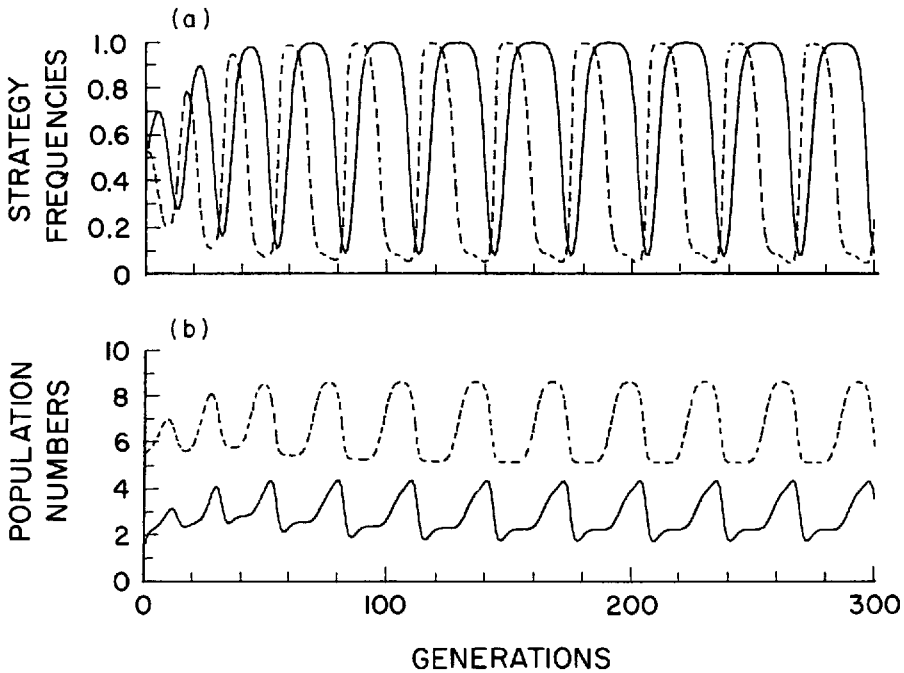


Figure 5. Results of a simulation of a prey-predator arms race game illustrating cyclical changes in behavior and the consequences for population trajectories. Panel (a) indicates the frequency of prey (---) and predator (—) behaviors and (b) indicates the resultant changes in prey (---) and predator (—) population numbers. Reprinted from Parker (1985) with permission.

Frequency-dependent Behavior.—Rather than maintaining fixed behavior through time, prey and predators may respond to the current behavioral state of their adversaries (Sih, 1984). Frequency-dependent behavioral responses may lead to evolutionarily stable strategies or to cyclical variations in behavior (Parker, 1985). Parker employed game theory to simulate the changes in frequency of prey and predator behaviors and their consequences for population change. Figure 5 reproduces the results of one such simulation where the behavioral “strategy” of the prey and predator depend on the behavioral state of their opponent. The predator can employ either low armament or high armament strategies and the prey either negligible defense or medium defense strategies. The behavioral states of prey and predator covary in a stable oscillation with a phase lag (Fig. 5a). These variations in behavior in turn promote an oscillation in numbers of individuals (Fig. 5b). Parker (1985) notes that the changes in behavior drive the numerical oscillation rather than the converse. This runs counter to the classical interpretation of density-dependent prey-predator oscillations, where the numerical changes in abundance are thought to force changes in behavior (e.g., through increased territoriality during crowding). In another application of game theory, Iwasa (1982) simulated diel vertical migration behavior as a prey-predator arms race where prey and predator behaviors were mutually dependent. Considerable further exploration can be made of the mutually responsive changes of prey and predator behavior.

Many of the avoidance, escape and defense responses of prey organisms can

be met or countered by predators. If particular species pairs interact extensively over long periods of time, then coevolution of behavioral traits of prey and predator might be expected to occur. Coevolved traits arise through reciprocal heritable adaptations (Futuyma and Slatkin, 1983). For example, sustained interaction between a prey and predator pair may result in modification of locomotory patterns or of diel vertical migration behavior. Such responses might be more common in low diversity plankton assemblages where the probability of a strong interaction involving only a particular pair of species is more likely than in a high diversity assemblage. Host-parasite relationships and symbiotic interactions, e.g., between hyperiid amphipods and their gelatinous hosts (Madin and Harbison, 1977; Harbison et al., 1977), are also likely situations for the evolution of coevolved behavior.

Closed ↔ Open Systems.—Some of the strongest evidence for the impact of predators on plankton communities has come from smaller lakes, field enclosures, fjords or embayments. In closed (or semi-closed) systems where the entire population is exposed to intensive predation pressure, predators may be a strong factor leading to behavioral adaptations of prey or to changes in the composition of a zooplankton assemblage. However, open systems such as oceanic environments and large lakes are not comparable in all respects to closed systems. The existence, and waxing and waning, of eddies, fronts, and other features introduce considerable heterogeneity into the physical environment of open systems (Haury et al., 1986). Zooplankton populations entrained in such features will be exposed to a heterogeneous predator, food and competitor environment. This heterogeneity may affect the characteristics of interactions with predators, e.g., by altered spatial overlap of prey and predators, or through the refuge from local extinction provided by lateral diffusion (Wroblewski and O'Brien, 1976). In addition, deep bathymetry may afford new opportunities for pelagic prey to attain deep water refuges. Accelerated understanding of the consequences of prey behavior for the dynamics of planktonic populations will require close attention to the setting where prey and predator interact in nature.

ACKNOWLEDGMENTS

Thanks are extended to G.-A. Paffenhöfer and H. J. Price for conceiving and convening this symposium. The travel support and symposium sponsorship provided by the Skidaway Institute of Oceanography are gratefully acknowledged. I thank L. R. Haury, M. R. Landry, M. M. Mullin and the symposium editors for their critical readings of the manuscript. Permission to reprint figures was granted by each of the authors, as well as the copyright holders: Figure 1—The University of Chicago Press; Figure 2—Martinus Nijhoff/Dr. W. Junk publishers; Figure 3—The American Society of Limnology and Oceanography, Inc.; Figure 4—IRL Press; Figure 5—Blackwell Scientific Publications Limited.

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DATE ACCEPTED: April 19, 1988.

ADDRESS: *Scripps Institution of Oceanography, A-027, University of California, San Diego, La Jolla, California 92093.*