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DIEL PATTERNS OF ZOOPLANKTON BEHAVIOR

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ABSTRACT

Zooplankton exhibit a variety of daily cycles including vertical and horizontal migrations, changes in feeding behavior and alternating reproductive states. The most popular hypothesis to explain the adaptive advantage of diel vertical migration is predator avoidance, i.e., nocturnal vertical migrations afford protection from visually feeding predators, whereas reverse (diurnal) migrations result from avoidance of nocturnally migrating, nonvisual predators. Proposed metabolic advantages of vertical migration have received much attention, but relatively little experimental support. Nocturnal migrations may also represent an adaptive behavior for avoidance of damaging solar radiation. One is struck with the variations in diel behavior patterns and the apparent plasticity of zooplankton in adapting diel behaviors to fit specific environments. Recent studies considering multiple causes of vertical migration show much promise. Problems and improvements in studies of diel zooplankton behavior are discussed.

Diel movements of zooplankton are widespread, conspicuous and probably one of the first behaviors noted for zooplankton (Bayly, 1986). This paper provides an overview of the present knowledge concerning diel patterns of zooplankton behavior and suggests some directions for future research. It is not a complete review of the literature in this field. Zooplankton behaviors treated here include vertical and horizontal migrations, diel feeding cycles, diel reproductive cycles and the effects of ontogenetic and seasonal changes on the aforementioned cycles.

VERTICAL MIGRATIONS

Definition of Patterns.—Hutchinson (1967) provides a thorough discussion of variations in the vertical movements of zooplankton. Most species, Hutchinson contends, rise to the upper waters at night as a "nocturnal" migration, or if they show two periods of maxima near the surface, the first is near dusk and the next near dawn, as a "twilight" migration. These patterns contrast with a "reversed" migration in which the animals move downward at night and return toward the surface in the day. It becomes obvious from the numerous variations cited by Hutchinson (1967) and other authors that there is a continuum of types from nocturnal to reversed. For simplification, I shall generally refer to the two extreme patterns, "nocturnal" and "reverse."

Reverse migrations are generally thought of as less common than nocturnal migrations; however, there are no quantitative data on the frequency of migration patterns to actually support this idea. Likewise, the percentage of lakes or oceanic regions exhibiting no migration is unknown.

Control Mechanisms.—The term control mechanism is used here to describe an immediate response by an individual zooplankter. This contrasts with the term adaptive mechanisms, used later, which implies a population level response that has some response time lag. These terms are equivalent to "proximate" and "ultimate" factors previously used to contrast immediate and long-term responses.

LIGHT. There appears to be little doubt that some feature of the daily light change provides the primary stimulus for timing the diel nocturnal migrations of most animals, i.e., light defines the temporal boundaries of the pattern (see reviews by Hutchinson, 1967; Banse, 1964; Forward, 1976). Since zooplankton also appear to have endogenous circadian rhythms (Ringelberg, 1964; Harris, 1963; Enright and Hamner, 1967; Ringelberg and Servaas, 1971), light probably acts as a zeitgeber that maintains the 24 h periodicity. Early laboratory studies of *Daphnia* by Clarke (1932; 1933) and later by Ringelberg (1964) indicated that light change provides the stimulus for the initiation of the upward migration. This idea has been supported with field studies on plankton in the ocean (Clarke, 1933) and in lakes (Haney and Hall, 1975). The rate of relative light change appears to control the rate of ascent of deep water marine zooplankton (Ringelberg et al., 1967; Stearns and Forward, 1984), as well as *Chaoborus* (Haney, 1987). Absolute light intensity may also be involved in the timing of the movement of *Chaoborus* out of the sediments (Swift and Forward, 1988). In addition to timing, light can also be important in determining the depth at which migrating zooplankton reside during the day (Clarke and Backus, 1956; Zaret and Suffern, 1976).

The general description of light control, although widely accepted, is not universal and cannot, for example, apply to reverse migration. One explanation of reverse migration is that animals undergo a complete reversal of light responses used by nocturnal migrators, swimming downward in response to decreasing light and preferring high light intensity near the surface in the day. A question of major importance is how such a reversal can be accomplished. Noting that reverse migrations of crustacean zooplankton were correlated with alkaline lakes with pH 8.2 in his and other studies, Bayly (1963) proposed that reverse migrations may be caused by a pH-induced positive phototaxis, as demonstrated by Loeb (1906) and later suggested by Baylor and Smith (1957). Bayly (1986) modified the pH hypothesis to include possible avoidance of photosynthetically-active cyanobacteria. It is difficult, however, to see the adaptive value of reverse migration under this hypothesis, for the highest photosynthetic rates and pH values would occur during the day when animals are in the upper water and lowest values should occur at night when they are in the deeper water. Numerous instances of reverse migration have also been recorded in the absence of extreme pH or other water chemistry (Bayly, 1986). In several instances predator avoidance appears to be involved in the migration reversal of marine (Ohman et al., 1983) and freshwater copepods (Fedorenko, 1975). In any case, reverse migration cannot occur unless the "normal" light response is overridden by some environmental factor or reversed through selection for genotypes with a reverse-phototactic response. In the former case, it is possible that overriding environmental cues may include mechanical or olfactory signs created by predators. Such "flight response" of the prey would require a suppression of the normal phototactic behavior. Nothing is known about genetic control of phototactic behavior of zooplankton. Much could be learned from closer investigation of the causes of reverse migrations, especially to determine whether light responses of zooplankton are genetically or environmentally controlled.

TEMPERATURE. Thermal gradients in the thermocline have been implicated as inhibitory to the vertical migration of zooplankton (Gehrs, 1974; Brunel, 1979; Southward and Barrett, 1983). However, frequent observations of migrating zooplankton moving through the thermocline clearly indicate that temperature change is not an effective barrier to some migrants. Avoidance of cold, hypolimnetic or warm, epilimnetic water is sometimes suggested as the reason a particular species has limited its amplitude of migration, but behavioral stenothermy has not always been observed in the field. A species may be associated with cold or warm temperatures in one lake, but show the opposite relationship in another. For example, *Daphnia ambigua* is commonly found in the cool metalimnion of lakes in the northeastern United States (Tappa, 1965), but is also common in subtropical Florida lakes (Brooks, 1957). *Daphnia magna*'s avoidance of cold water in laboratory experiments lead Calaban and Makarewicz (1982) to suggest that daphnids in nature may limit their vertical migration in response to cold hypolimnetic water. However, it is not uncommon to find *Daphnia* migrating in and out of cold oxygenated hypolimnia. Rudyakov (1975), using marine copepods and ostracods, and Gerritsen (1982), using lake *Daphnia* species, found that upward swimming increased in response to increasing temperature. These authors concluded that an encounter with a thermocline should enhance the rate of ascent and descent of migrating animals.

In temperate lakes, water temperature appears to have only modifying effects on the pattern of vertical migration. In contrast, temperature can be of primary importance in regulating the diel migration under summer conditions in the Arctic, when daily variations in light are inadequate as a zeitgeber (Buchanan and Haney, 1980). These authors found that *Daphnia middendorffiana,* a species common in tundra ponds, showed no response to low temperatures, but moved downward as temperatures increased above 10°C. In contrast, *D. magna,* an introduced, temperate species, moved upward with increasing temperature in water less than 10°C. Such a temperature controlled migration of *D. magna* would also be predicted by Gerritsen's results, for in a shallow pond, increasing daytime temperatures should cause *Daphnia* to swim quickly, moving up while cooling temperatures should cause slower swimming and therefore downward drifting. One might expect this effect in temperate ponds, but its influence on vertical distribution is probably masked by the influence of light.

FOOD. The division of factors as either control mechanisms or ultimate causes (adaptive significance) is probably least useful for food. The importance of food in vertical migrations of zooplankton is often used in evolutionary arguments. There is also compelling evidence that food can also act as a proximate cause for migration by influencing the timing of migration as well as the depth distribution of animals.

Gauld (1953) proposed that food abundance mediated through hunger or satiation could act as the proximal signal for upward and downward migrations of marine copepods. There has been support for this hypothesis from field studies of chaetognaths (Pearre, 1973; 1979), marine planktonic ostracods (Arashkevich, 1977) and copepods (Mackas and Bohrer, 1976; Conover et al., 1988). A modified hypothesis of hunger-cycle control of the timing of copepod migrations was later suggested by Enright and Honegger (1977).

Early laboratory studies found that *Daphnia* were more positively phototactic when starved (Clarke, 1932). Extrapolating this finding to field conditions, one might expect *Daphnia* to occupy shallower depths under low food conditions. This prediction is supported by the recent work of Johnsen and Jakobsen (1987). Using additions of yeast to increase food concentrations in lake enclosures, these authors found that *Daphnia longispina* deepened their day-depth distribution and underwent greater diel migrations with increasing food. At low food abundance, animals occupied shallower depths and had reduced vertical migration. These results were interpreted as evidence for control of phototaxis by hunger, rather than genetic selection for clones of *Daphnia* with different phototactic responses as suggested by Dumont et al. (1985).

OTHER CUES. There is mounting evidence that zooplankton can discriminate foods on the basis of chemoreception (DeMott, 1986). Although genetic selection is generally proposed to account for shifts in migration patterns, it is also conceivable that chemically stimulated responses could provide zooplankton with the ability to make rapid behavioral adjustments to changes in food quality or the proximity of predators. Mechanoreception or visual cues could also enable zooplankton to detect predators and make changes in their swimming orientation. Such responses would be most important in tailoring the migration pattern to small scale spatial heterogeneities in each lake rather than directing the migration over long distances.

Adaptive Significance.—PREDATOR AVOIDANCE. It is frequently assumed, a priori, that low light conditions at night can provide protection for some zooplankton from fish predators (Hutchinson, 1967; Wright et al., 1980). There can be little doubt that predation can be an important force in selecting for vertical migration behavior in zooplankton. The idea is not new. Some of the earliest research on zooplankton migration suggested the movement of animals into the deep water during the day was to avoid predators in the upper, better lighted waters (see review by Bayly, 1986). More recently, persuasive arguments have been made for the importance of visually feeding fish in selection for the "typical" nocturnal migration in lakes (Zaret and Suffern, 1976; Hall et al., 1979) and marine systems (Vuorinen et al., 1983; Fancett and Kimmerer, 1985).

It is not yet clear how much time is required for predators to modify the pattern of diel vertical migration, nor whether such modifications can occur only through genetic selection. Gliwicz (1986) demonstrated the long-term influence of fish predation on vertical migration in the mountain lakes of Poland. The degree of vertical migration was proportional to the length of time since stocking with fish, and in the lakes not containing fish the zooplankton did not migrate. On a shorter time scale, Luecke (1986) documented the shift from non-migrating to vertically migrating *Chaoborus flavicans* within a decade in Lake Lenore, Washington. Luecke proposed that this change in migratory behavior was the result of selection against the non-migrating morphs by cutthroat trout rather than an immediate behavioral response by *Chaoborus* to optical or olfactory cues. Stich and Lampert (1981) suggested that fish predation may have selected for the gradual increase in the amplitude of migration of *Daphnia galeata* from spring to fall in Lake Constance, indicating that genetic selection may occur within a single season. In contrast, experimental manipulations of algal food and fish within enclosures in Lawrence Lake, Michigan, resulted in rapid changes in vertical migration of *Daphnia* that appeared to be due to direct sensory response, rather than genetic shifts in the population (Leipold, pers. comm.).

An assumption of the predation hypothesis is that visual planktivores feed most efficiently at high light intensities, thereby selectively removing zooplankton that remain in the upper waters by day. Small zooplankton species and immature animals may stay in the lighted waters because of their reduced visibility due to their small size. As larger zooplankton move up into the water column at dusk and down at dawn, they are subjected to a brief period of fish predation, but during the night nocturnal migrants are protected by darkness. Variations in the movement and feeding of the planktivorous fish should influence the migration pattern of the zooplankton. There is much variation in the diel movements of visually feeding fish. For example, *Notemigonus crysoleucas* school in the shallow littoral zone in the day and move into the open water at night (Zaret and Suffern, 1976; Hall et al., 1979), whereas the peamouth chub, *Mylocheilus caurinus* (Northcote et al., 1964), and the sockeye salmon, *Oncorhynchus nerka* (Eggers, 1978), can undergo limnetic nocturnal vertical migrations throughout most of the summer. Facultative feeding by the predator and high prey density should contribute to the stability of the nocturnal migration pattern. Feeding on multiple resources allows the predator to supplement its "bonus" feeding at twilight with daytime feeding in the littoral or on the bottom. When zooplankton biomass is high, fish can obtain their food requirements during brief feeding bouts at dawn and dusk (Eggers, 1978). Most importantly, under both situations, predation pressure from fish can be intensive, but limited to short bouts at twilight, thereby maintaining a precise control on the timing of migration.

The effect of non-visual predation, such as tactile-feeding invertebrate predators (e.g., copepods, chaoborids, chaetognaths, ctenophores and siphonophores) and certain fish (e.g., gizzard shad), is less well documented. The resultant zooplankton migration pattern depends upon the vertical distribution and migration pattern of the predator. Reverse migrations of freshwater calanoid copepods appear to be often related to intense predation by *Chaoborus* (Hairston, 1980). For example, in Eunice Lake, British Columbia, *Diaptomus kenai* moved downward at night apparently in response to predation by *Chaoborus trivittatus,* since *D. kenai* was a preferred prey of *Chaoborus* and the reverse migration provided a spatial refuge from the nocturnally migrating *Chaoborus* (Fedorenko, 1975). In Dabob Bay, Washington, the marine *Pseudocalanus* sp. appears to employ reverse migration as a predator-evasive response to predatory chaetognaths and copepods that undergo the nocturnal vertical migrations (Ohman et al., 1983). There is an unmeasured, but implied, second level of predatory influence that is necessary to explain why the chaoborids and chaetognaths do not simply follow their prey upward in the day. The need to consider multiple levels of predators is evident.

METABOLIC ADVANTAGES. Since the phytoplankton production in most systems is greatest in the upper, well-lighted waters, it is generally assumed that the most favorable feeding conditions for zooplankton herbivores is in these regions. To explain a non-predatory advantage of spending part of the day below this food-rich, optimal zone, McLaren (1963) proposed that zooplankton spending the night in warm water should increase feeding rates while utilization of the ingested food be enhanced in the cool water during the day, thereby giving the migrating animal a "metabolic bonus" or advantage over non-migrating species. Despite the interest this appealing argument has generated, attempts to support the idea have failed in the laboratory (McLaren, 1974; Stich and Lampert, 1984; Orcutt and Porter, 1983; Lampert et al., 1988), as well as in the field (Frost, 1988).

Enright (1977) proposed that migrating marine copepods could gain a metabolic advantage by compensatory high feeding rates at night in response to hunger during the day. This hypothesis is supported by the well-defined hunger responses of marine calanoid copepods (Runge, 1980) and by the elevated nocturnal feeding by cladocerans (Haney, 1985). Curiously, calanoid copepods in lakes appear to have little diel variation in feeding rate (Haney and Hall, 1975).

Dagg (1985) recently rephrased the question to ask under what food conditions animals can "afford" to migrate, rather than whether there is a feeding advantage to migration. His hypothesis predicts that when food concentration is high, migrating animals can make up the costs of migrating. It is significantly different from previous metabolic models since it assumes that food is a modifier of vertical migration, but not the driving force. There is no convincing support yet for this idea and it appears to contradict Hutchinson's (1967) observation that, "In general diurnal migration is best observed in deep, unproductive transparent lakes," since one would assume that such lakes have low food concentrations.

The importance of food in regulating vertical migration in nature is not easily discerned from either laboratory or field studies. Simulations of food and temperature fluctuations in the lab using *Daphnia* from Lake Constance led Stich and Lampert (1984) to conclude high food concentrations would promote vertical migration of *Daphnia galeata.* In a subsequent field study of Lake Constance zooplankton, Geller (1986) concluded that *Daphnia* should begin to migrate vertically when food becomes scarce. Clearly, we are only at the beginning of our understanding of the role of food in regulating diel vertical migration.

For most natural systems it is unrealistic to consider a single factor such as food or predation as the cause of diel vertical migration. Rather, the pattern of migration must represent the summarial effect of multiple factors and the resultant migration pattern can be viewed as a tradeoff between conflicting selective forces (Gliwicz, 1986). In an unusual field study that included interactive effects of food and fish predation on vertical migration, Gliwicz and Pijanowska (1988) found that the extent of vertial migration could be influenced by both of these factors. In lakes with similar food conditions, *Cyclops abyssorum* migrated only where planktivorous fish were abundant. In lakes with similar abundances of planktivorous fish, populations of *Daphnia hyalina* migrated vertically only in lakes with a high ratio of epi- to hypolimnetic food. An instructive lesson from this study is that neither food availability for zooplankton nor predation intensity would have accounted for the variations in migration behaviour if they had been considered alone.

Additional support for the "tradeoff" hypothesis of Gliwicz was found by Johnsen and Jakobsen (1987) in their study of a small pond with intense predation by small salmonids. There it appeared that the force of starvation was stronger than the predator-avoidance behavior, since under low food conditions *Daphnia* moved to the surface at the expense of greater risk of fish predation, rather than starve in the deep, light refugium.

LIGHT-DAMAGE AVOIDANCE. Although light avoidance was among the earliest reasons given for the behavior of vertical migration (Huntsman, 1924), it received little support or interest until the last decade. Since then, it has been well documented that damage from solar radiation can be an important selective force in nature (Ringelberg et al., 1984) and that red carotenoid pigmentation protects copepods from damage by ultraviolet (Ringelberg et al., 1984) and visible light (Hairston, 1976; 1979). Similar protective effects of pigmentation were demonstrated with cladocerans (Siebeck, 1978). It has also been shown that damaging ultraviolet light penetrates several meters deep in clear oceans (Damkaer et al., 1980; Siebeck, 1981) and lakes (Ringelberg et al., 1984). From these studies one can conclude that pigmentation can provide zooplankton with a means of inhabiting the upper, well-lighted waters. In such instances it must be assumed that the greater predation risk due to high visibility of pigmented animals is offset by effective escape responses of copepods, or the absence of visual predators. Also, it is easy to see why unpigmented zooplankton cannot inhabit shallow waters in clear lakes and oceans.

However, the above studies have not shown a direct causal relationship between light-damage and diel vertical migration. An attempt to demonstrate a direct link between light damage, light response and vertical migration was made by Pennington and Emlet (1986). These authors contended that the diel vertical migration of starfish pluteus larvae is directly regulated by daily changes in the UV-B light. Pluteus stages of *Dendraster excentricus* stop swimming when irradiated with UV light. Thus, the authors conclude that photoresponse of pluteus larvae is directed by UV-B light and the resultant nocturnal migrations effectively remove pluteus larvae from the UV zone. This example illustrates that the same factor may act directly in adaptive selection as well as serve as an environmental cue.

There are still many unanswered questions concerning light-damage and zooplankton vertical distribution. Not all animals that occupy the upper water by day and undergo reverse migrations are pigmented. It is possible such animals could be protected by making short forays in and out of the light-damaging zone during the day, balancing the risk from light exposure with the benefits of higher food levels. Such vertical movements could only be identified by observation of individual animals and would not be resolved by usual population sampling techniques. Also unexplained is the means by which at least a portion of immature animals inhabit near-surface waters (see examples in Hutchinson, 1967). Random downward mixing of small animals with lesser swimming abilities in the epilimnion could afford protection from continuous exposure to high light intensities. It is also possible that immature animals have evolved a higher tolerance to light that permits them to inhabit shallow waters. At this time, however, such mechanisms have no experimental support.

Genetic Control. —There is little experimental evidence to support the contention that diel behavior patterns are controlled genetically; yet the validity of many evolutionary hypotheses depends on assumptions that observed changes in migration are the result of selection for specific genotypes (Stich and Lampert, 1981; Luecke, 1986). Because of the high reproductive rates of many zooplankton, one can argue that rapid changes in diel behavior are due to genetic shifts or behavioral plasticity or a combination of these forces.

A few cases linking migration behavior to genetic control have been recently documented. In a study of shallow farm ponds, Weider (1984) identified different clones of *Daphnia pulex* that exhibited distinct vertical distributions within the same pond. Dumont et al. (1985) were able to isolate populations of *Daphnia magna* with different light responses, demonstrating that there can be genetic control of phototaxis in *Daphnia.*

There appears to be even less information on genetic control of other diel behaviors such as feeding and reproduction. Since these behaviors depend on different organ systems (e.g. photosensitivity, feeding mechanisms and reproductive activities), it would be valuable to know whether they can undergo independent genetic selection and, if so, whether this could account for independence of migration and feeding patterns observed in nature (see discussion under Feeding Activities).

HORIZONTAL MIGRATIONS

Movements of fish from the littoral region in the day to the open water at dusk are well known (Hall et al., 1979). Plankton net hauls from lakes at night often contain benthic and littoral invertebrates such as mayfly nymphs and notonectids suggesting a daily invasion of littoral animals into the limnetic zone. There is, however, little published information on diel horizontal movements of littoral or limnetic zooplankton.

Polyphemus pediculus form dense patches in the shallow littoral region of Stonehouse Pond, New Hampshire, in the day, but move into the open water at night (Mattson, 1978). Mattson suggested that this diel horizontal migration is caused by active aggregation of *Polyphemus* by day and random movements at night in the absence of adequate light cues. The reverse movement should occur for limnetic species allowing them to move into littoral regions at night when light intensity is inadequate for shore-avoidance (Siebeck, 1964). Burckhart (1910) proposed that such a sequence of diel horizontal movements should result from downward migrating animals following the contours of the lake and should serve to effectively remove limnetic zooplankton from the adverse conditions of the littoral during the day. Such diel movement into the littoral at night and back into the limnetic in the early morning has been documented for *Chaoborus flavicans* larvae in a small lake (Franke, 1987).

An unusual horizontal movement was suggested by Timms and Moss (1984), who postulated that limnetic species, *Daphnia longispina* and *Bosmina longirostris,* avoid fish predators by concentrating amongst littoral water lillies (Nuphar and Nymphae) in the day and moving out into the open water in the evening. Although the authors do not present direct evidence for this migration, they raise some interesting points. First, their observation of large members of limnetic cladocerans in the lilly beds shows an exception to the principle that open water zooplankton actively avoid the shoreline by "Uferflucht" (Siebeck, 1964). Secondly, it suggests that where there is a dominance of open water planktivores in a shallow system such as the Broadlands (Z_{max} 1.5 m) that lacks a deep water refuge, zooplankton may respond by essentially adopting a "reverse horizontal" migration as a predator defense.

Hamner et al. (1982) described 1-km daily migrations of scyphomedusan *Mastigias* to opposite ends of Jellyfish Lake, a meromictic lake on the island of Palau. This horizontal migration appeared to be a means of maximizing exposure of its symbiotic zooxanthellae to sunlight. In addition, *Mastigias* underwent reverse diel migrations into the chemocline to absorb nutrients for its zooxanthellae. This highly unusual situation illustrates how both horizontal and vertical migrations can provide an organism with "metabolic advantages."

A cycle of seasonal shifts in the horizontal distribution of *Polyphemus* have been described (Mattson, 1978), in which the population is strongly littoral in the spring, moves into the open water in the summer and back into the littoral in the fall (Fig. 1). The summer movement into the limnetic may have been due to increased predation by littoral fish fry, since *Polyphemus* is highly visible and readily eaten by rainbow trout in Stonehouse Pond. Coupled with Timms and Moss (1984), these examples illustrate the "plasticity" of horizontal movements, daily and seasonally. Given adequate selective pressure, limnetic species may become littoral and littoral species may become limnetic.

FEEDING ACTIVITIES

Heightened foraging activity is associated with the nocturnal habits of many terrestrial herbivores and carnivores. It might not be surprising, therefore, to find increased feeding activity of zooplankton during nocturnal migrations.

From the small body of literature available, one can conclude that diel feeding cycles can be measured in the laboratory with *Daphnia* in both cultures (Starkweather, 1975; 1983) and freshly collected animals (Chisolm et al., 1975; Duval and Geen, 1964; Haney, 1985). It is not known, however, how long and under what conditions feeding rhythms persist in the laboratory. Diel rhythms of feeding (Reeve, 1964; Chisolm et al., 1975; Starkweather, 1983), vertical movements (Harris, 1963; Enright and Hamner, 1967) and photosensitivity (Ringelberg and Servaas, 1971) have been found with no light change in the laboratory, demonstrating these activities have an endogenous component.

There is much evidence that a wide variety of herbivorous copepods feed most intensively at night during the course of vertical migration (Gauld, 1951; Petipa, 1964; Singh, 1972; Mackas and Bohrer, 1976). Large, omnivorous zooplankton such as euphausiids (Sameoto, 1980) and chaetognathes (see review by Feigenbaum and Maris, 1984), feed more at night, although instances of no feeding rhythms have also been observed (Hu, 1978). Since feeding activities were based on the gut contents of animals captured at different times of the day, actual feeding

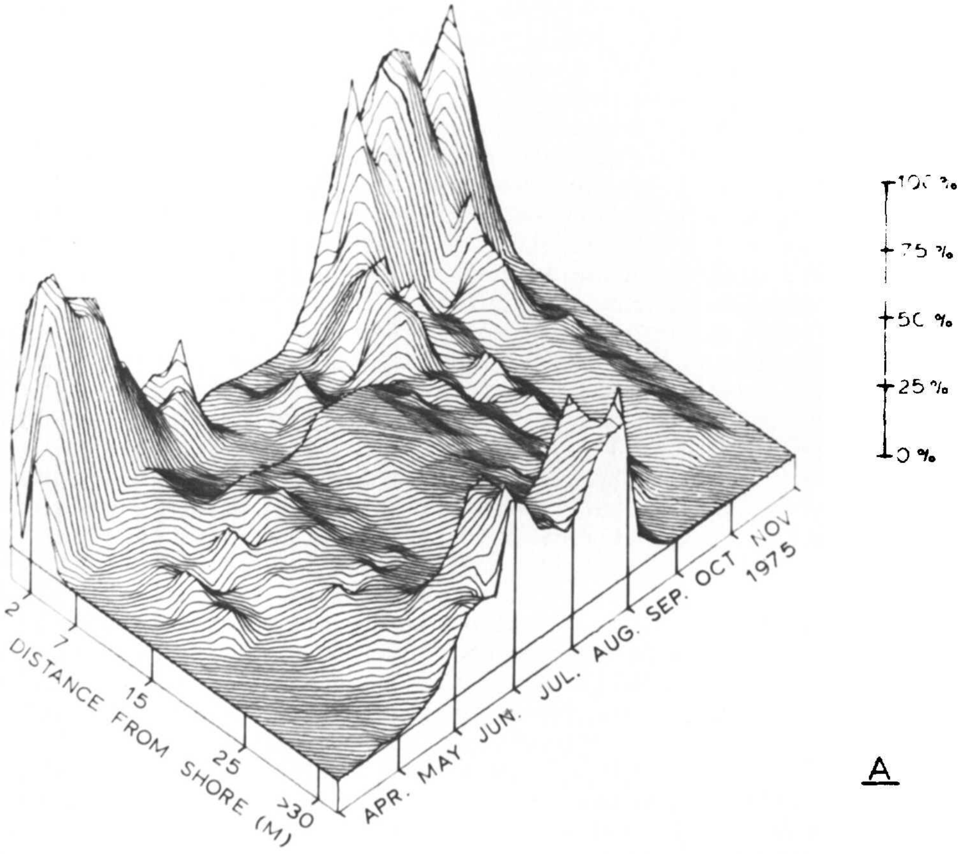

Figure 1. Seasonal and spatial changes in the abundance of *Polyphemus pediculus* in Stonehouse Pond, New Hampshire. Reprinted from Mattson (1978) with permission.

rates cannot be determined without knowing the retention time for the food in the gut. It is also possible that day/night differences in gut contents simply reflect the greater abundance of food in the upper waters.

It is difficult in nature to determine whether nocturnal feeding is due to a light-controlled rhythm or simply the positive response to better food conditions in the upper waters. Marcus (1988) provided evidence that the effects of photoperiod can override the effect of food abundance. The marine copepod *Labidocera aestiva,* cultured under a light–dark cycle in the laboratory, had twice the fecundity when they received food during the dark than if they received food only during the light cycle. Apparently, *Labidocera* were not able to reverse their feeding cycle to fully utilize food when it was available.

In a study of vertical migration behavior of zooplankton in the English Channel, Harris (1988) found that migrating zooplankton sometimes simply passed through a deep layer of chlorophyll, supporting the idea that food was not the primary regulating factor. However, other behaviors were also observed by Harris, including migrations of zooplankton into the chlorophyll maximum at night or in the day, and permanent residence in this food-rich layer by non-migratory zooplankton. This example illustrates the ability of zooplankton to use a variety of strategies for a given set of environmental conditions. The question remains: how do certain species adopt a particular strategy?

In situ measurements of filtering rates of zooplankton can give a clearer picture of their daily changes in feeding activities. Elevated nocturnal filtering and ingestion rates have been measured in situ for mixed zooplankton (Duval, 1973), *Daphnia* (Nauwerck, 1959; Haney and Hall, 1975; Haney, 1985) and *Holopedium* (Haney, 1985). As one might expect from the reduced or absent vertical migrations in most immature zooplankton, nocturnal increases in feeding are most pronounced in the largest *Daphnia* (Haney and Hall, 1975), resulting in significant differences in body size : filtering rate relationships with time of day (Haney, 1985). This study also showed that smallest *Daphnia* have a dampened oscillation of feeding with time of day, but their period of nocturnal feeding is longer, representing a diel behavior that temporally compensates small animals for their disproportionately low filtering rates. This also agrees with observations that young *Daphnia* often migrate upward earlier and downward later in the morning than adults (Juday, 1904).

Not all in situ diel studies have found differences with time of day. Zooplankton community grazing, particularly, must be interpreted carefully, as these generally contain a mixture of species, some of which may not have pronounced feeding rhythms. For example, calanoid copepods in freshwater have much smaller diel variations in feeding than cladocerans such as *Daphnia* (Haney and Hall, 1975). Differences in the dominance of these two groups appear to have accounted for higher nocturnal community grazing when *Daphnia* and *Ceriodaphnia* were dominant but the absence of diel differences when *Diaptomus* was abundant (Haney, 1973). Similarly, Lampert and Taylor (1985) found no differences in grazing per unit biomass of the zooplankton community in Schöhsee, a lake dominated by *Eudiaptomus,* whereas Haney and Lampert (unpublished data) did find diel differences in *Daphnia cuculata* and *D. longispina* feeding in the same system, when individual rather than community grazing rates were measured. In situ grazing studies of Chow-Fraser and Knoechel (1985) and Knoechel and Holtby (1986) in lakes in southern Ontario showed no significant differences in feeding day or night for non-migrating planktonic cladocerans or copepods.

It is not obvious what factors may explain these differences in diel feeding behavior between studies, since the techniques used were virtually identical. However, the lakes in which no diel feeding differences were found had low food concentrations, the zooplankton were small-sized and showed little tendency to migrate (Knoechel, personal communication), whereas the lakes studied by Haney and Hall (1975) and Haney (1985) were mesotrophic to eutrophic with strong migrations of large-sized zooplankton. It is likely that the diel changes in small animals were undetectable and at very low food concentrations, cladocerans simply filter at their highest possible rates to minimize starvation, and that elevated nocturnal feeding is only possible when food is abundant (cf. hypothesis of Dagg, 1985).

Almost perfect correspondence of the patterns of vertical migration and changes in the filtering rates of *Daphnia* (Haney and Hall, 1975) suggests the two activities are closely coupled in nature. Closer examination of this inference is important, since a knowledge of both activities is crucial to an evaluation of the advantages of vertical migration. There are several observations, however, that suggest that feeding and migration are highly independent activities, allowing for much variation in nature.

Marine herbivorous copepods appear to be largely nocturnal feeders, irrespective of migration behavior. For example, gut fullness of copepods in the North

Pacific central gyre indicated that both migrating and non-migrating animals had higher feeding rates in the night than in the day (Hayward, 1980). Using on-board radioisotope experiments to determine feeding, Daro (1985) found that in the North Sea *Calanus* did not migrate vertically, but did significantly increase its feeding at night. Likewise, *Oithona* did not migrate, but had highest feeding rates at 0200 and 1400. Dagg and Walser[1] (unpubl. in this symposium) found that although feeding and diel vertical migration were closely coupled for *Metridia,* there was a 3–4-h lag between arrival of *Calanus* at the surface and subsequent initiation of nocturnal feeding.

Similar examples can be found for lake cladocerans. In the small, mesotrophic Little Mill Lake, Michigan (Haney and Hall, 1975) winter and spring populations of *Daphnia pulex* underwent vertical migrations and elevated night feeding. In the summer, *Daphnia galeata* migrated vertically from the metalimnion to the surface and also increased its feeding at night. The *D. pulex* populations at that time did not migrate out of the hypolimnion but continued to have higher night-time feeding rates. Independence of migration and filter-feeding was also seen in the mesotrophic Schöhsee (Haney and Lampert, unpublished data). Filtering rates of *Daphnia cuculata* and *D. longispina* increased as the animals began to move upwards from the metalimnion (Fig. 2). A deep water population of large *Ceriodaphnia* sp. did not move vertically, but likewise increased their filtering at night. In a further example, during midsummer in the Arctic, zooplankton in the deep lakes were stratified vertically, but did not change depth with time of day (Buchanan and Haney, 1980), presumably because of insufficient light changes to evoke vertical migrations. Filtering rates, however, do change with time of day (Fig. 3), with regular, daily oscillations unrelated to the spatial distribution of the population. These examples of independence of feeding and migration activities strongly suggest that diel vertical migration results largely from a phototactic (oriented) response to light, whereas feeding rates are controlled photokinetically (non-directed). With strong light changes at dusk and dawn, there should be coincidence in migration and feeding in populations of zooplankton that migrate. The result is a greater variability in migration patterns than in feeding rhythms.

REPRODUCTIVE CYCLES

Since vertical migrations of zooplankton often expose migrating animals to daily oscillations in temperature it might be expected that other activities such as development and reproduction would exhibit daily rhythms. Diel cycles of egg deposition have been recorded for marine copepods, *Calanus* (Harding et al., 1951; Runge, 1985). Egg laying and hatching are synchronized with time of day for freshwater rotifers *Brachionus, Keratella* (Saunders, 1980; Magnien and Gilbert, 1983) and *Hexarthra* (Ruttner-Kolisko, 1978) as well as the cyclopoid *Mesocyclops* (Gophen, 1978) and *Daphnia* (Brubaker, 1972). Hatching rates are generally higher at night, due to the warmer water encountered by nocturnal migrators (Brubaker, 1972; Magnien and Gilbert, 1983), resulting in deposition of young in the upper waters at night. Possible influence of location of young at the time of hatching and subsequent migratory behavior developed by these young animals is not known. Reverse migrations can have the opposite effect with synchronized daytime hatching and greater numbers of young placed in the deeper water. Egg-bearing *Keratella crassa* collected from the lake and kept in the laboratory under

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[1] Dagg, M.G. and W.E. Walser, Jr. Relationships between feeding activity and diel migration in *Calanus pacificus* and *Metridia pacifica*. Unpublished paper presented at this symposium.

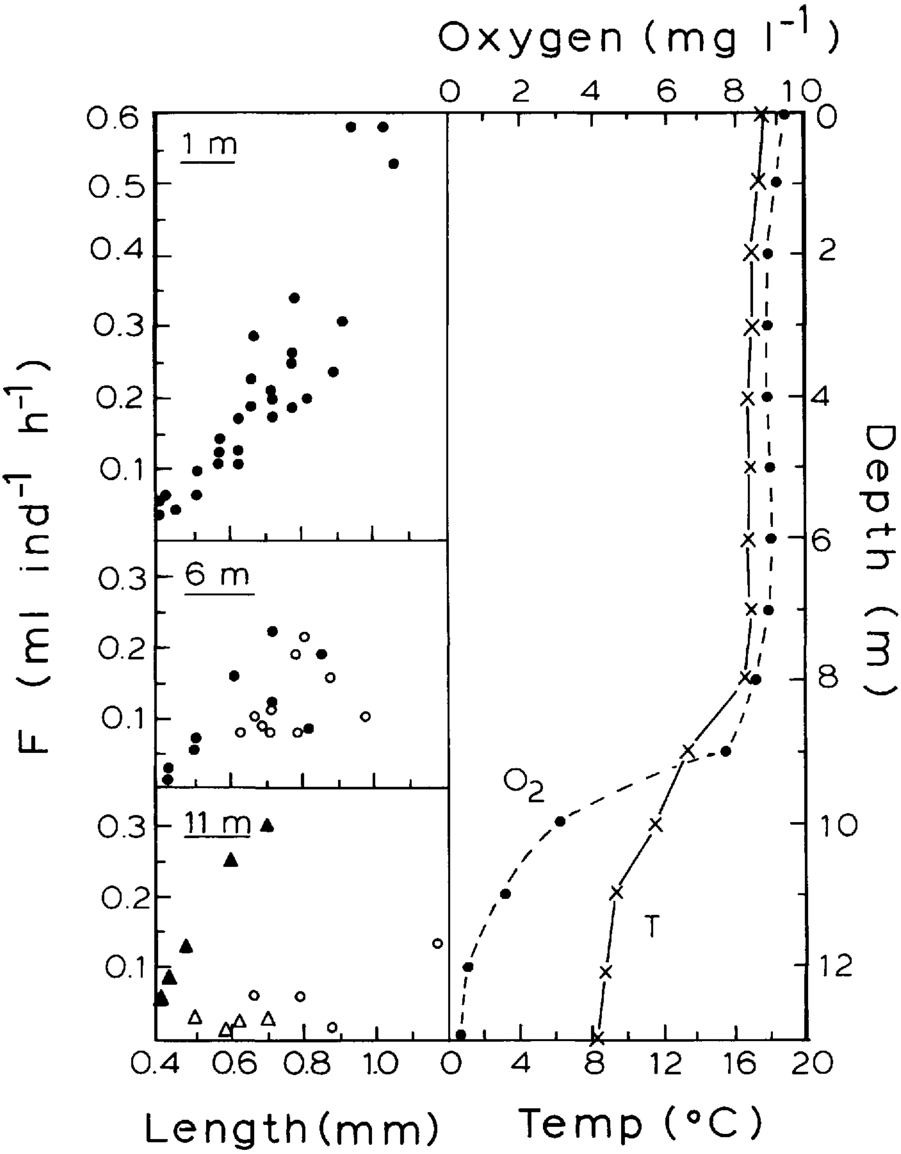

Figure 2. Changes in the relationship between filtering (F) rate and body size of migrating *Daphnia cucullata* and non-migrating *Ceriodaphnia reticulata* by day (1500–1600) and night (2000–2300) in Schöhsee, Plön. Location of each F: graph denotes vertical position of the zooplankton in relation to the profiles of temperature and oxygen. Note the changes in filtering rates of *Ceriodaphnia*, despite its failure to migrate vertically. Open symbols, day; closed symbols, night.

constant temperature show the same hatching synchrony as animals in the field (Magnien and Gilbert, 1983).

Reproductive state may also influence the extent and timing of vertical migration. Magnien and Gilbert (1983) found that ovigerous *Keratella crassa* had a 4–6-h lag in the time of migration. The authors suggested this difference was not due to greater weight of animals with eggs and that it probably represented dif-

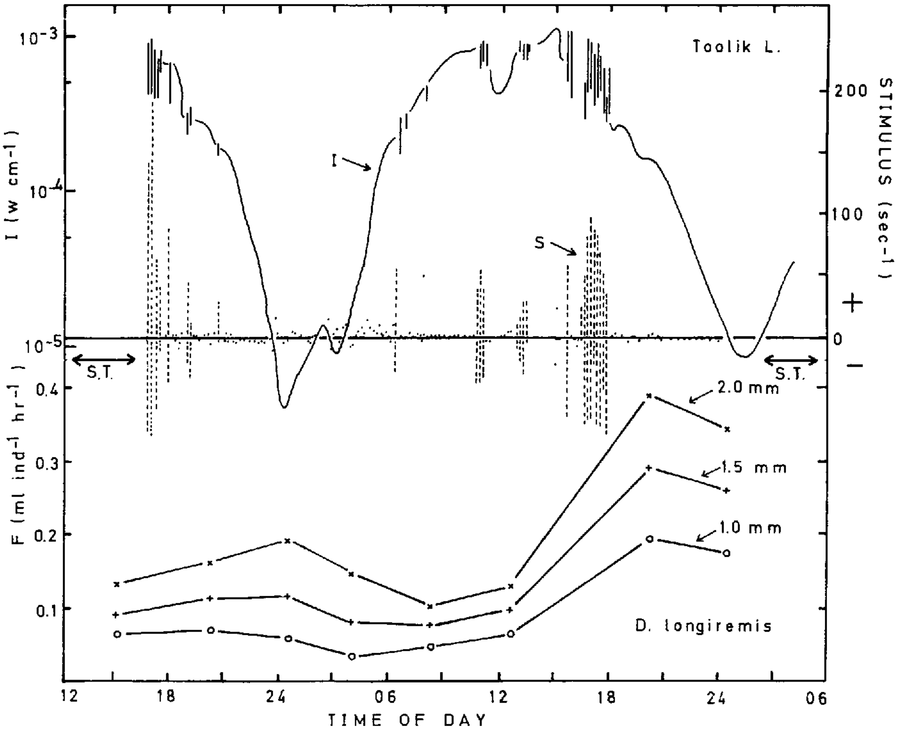

Figure 3. Filtering rate changes of *Daphnia longiremis* in the deep (Z_{max} = 50 m), arctic (latitude 68°N) Toolik Lake, Alaska. Filtering rates measured with in situ grazing chambers using ^{32}P-labelled *Rhodotorula* yeast. Populations of *D. longiremis* and other zooplankton did not migrate vertically during this period in mid-July (Buchanan and Haney, 1980) indicating the independent control of feeding and migration.

ferences in the animals' response to environmental factors regulating the migration. In the study of Three Lakes, Michigan (Haney and Hall, 1975) egg-bearing *Daphnia pulex* migrated at night into the epilimnion with more than twice the frequency of eggless females. Conceivably, the more pronounced migration of females with eggs could simply be a reflection of the higher nutritional state and vigor of animals with eggs or, conversely, the better nutrition of migrating animals. Egg-bearing *Daphnia* could also have a more sensitive photoactive response that exaggerates migration behavior. Curiously, male *D. pulex* remained in the intermediate depths and did not migrate into the epilimnion at night. Differential migration of males could have important implications and may help explain the cycle of seasonal changes in migration in Lake Constance (Stich and Lampert, 1981; Geller, 1986), where *Daphnia* populations gradually shift from non-migrating to migrating from spring through the summer. Preferential mating of non-migratory males with non-migratory females in the summer and fall may produce ephippial populations that have a reduced tendency to migrate. This would result in the lack of or reduced vertical migration of exephippial animals in the early spring. It could also have adaptive advantages by allowing the spring population to stay in algal-rich strata the entire day in the period before hatching of fish and intensive zooplanktivory (Geller, 1986). Increasing feeding by visual predators throughout the summer could gradually select for greater amplitudes of migration, especially by large, egg-bearing adults, thereby repeating the annual cycle.

DISCUSSION

Examinations of decades of investigations of zooplankton migrations has led many authors (see Bayly's list, 1986) to conclude that there are multiple causes for vertical migrations, in different, as well as within a single system. It is humbling to discover that this is largely a confirmation of Juday's (1904) conclusion based on a one-year study of 30 Wisconsin lakes that, "Each lake possesses factors peculiar to itself and the crustacea respond to these differences in environment in a greater or lesser degree. As a result, the diurnal movement in each lake has certain individual characteristics . . . the variation (in migration) is no greater, however, than one should expect from the great diversity of ecological factors involved."

Problems of Sampling.—Most field studies of diel activities are limited by the methods of data collection and analysis. Estimates of spatial displacement from distribution statistics of migrating populations are often inaccurate and may be misleading when populations do not migrate as a cohesive unit (Pearre, 1979). These problems are generally exacerbated by too few samples and broad observation intervals. For those researchers who have conducted diel studies it is no surprise that much of the field research on vertical migration have been based on sampling designs that are conspicuously inadequate. Generally, the sampling density in space and in time necessary to provide the desired resolution of population movements is prohibitively expensive and rapidly exhausts the investigators.

Selection of a sampling method adequate to achieve the goals of the investigation is important. Pumps are simple to use and provide rapid sampling, but may not efficiently catch strong swimming zooplankton. Pearre (1979) suggested the use of stationary traps for they allow for the detection of the direction of movement. However, such devices may be difficult to operate under field conditions, especially in marine studies (Harding et al., 1986). In shallow lakes, a tandem system of Schindler-Patalas type samplers could permit instantaneous depth profiles and allow more frequent sampling intervals. It is important to recognize that appropriate sampling gear for migration studies cannot be purchased; most often, it must be designed, built and tested by the researcher.

Experimental Methods for Diel Studies.—Field enclosures have been used to examine the changes in vertical distribution and migration of zooplankton (Johnsen and Jakobsen, 1987). This approach has the advantages of experimental replication and allowing manipulation of selected parameters such as food and predators, while maintaining ambient temperature and photoperiod. Enclosures do not, however, alleviate the above-mentioned sampling problems, especially when many enclosures are used.

Large tanks of water held indoors (plankton towers) have been especially useful in making direct observation of large marine organisms such as the scyphozoan jellyfish *Aurelia* (Mackie et al., 1981), using portholes in the sides of the tanks. Experiments with smaller zooplankton must deal with field-type problems of sampling (Conover and Paranjape, 1977). Multiple sampling approaches can be used in intermediate sized plankton towers by combining observation ports and sonar (Lampert's "Plön towers" in Price et al., 1988).

Direct observation of migration-related behavior of zooplankton in vessels in the laboratory is a useful, but deceptively simple experimental tool. The approach is not new and many early experiments elucidated some very fundamental properties of light responses of zooplankton such as *Daphnia* (Clarke, 1932; Heberdey and Kupka, 1942; Ringelberg, 1964). Light-induced artifacts are probably the most serious problem in the laboratory. Studies designed to observe migration behavior must take care to simulate light conditions with angular light distributions comparable to those found in nature (see experimental designs of Buchanan et al., 1982; Stearns and Forward, 1984). It is surprising that this technique has not been more intensively utilized and that many of the early experiments were never repeated or improved.

Remote sensing with sonar is attractive for it is ideally suited for synoptic surveys and continuous monitoring of population movements. However, acoustical tracking is best suited to systems where the target organism has a high sonar reflectivity such as *Chaoborus* (Northcote, 1964; Teraguchi and Northcote, 1966). Certain population features such as the upper boundary and modal points of the population can be quantified from the sonar traces (Haney et al., in press). The greatest limitation is the difficulty of identifying the specific organisms responsible for signals, since in nature there are often numerous zooplankters with comparable reflectivity. The use of a range of transponder frequencies can improve resolution, but frequent sampling with conventional methods must be used to provide necessary calibration. A relatively unexplored area is the adaptation of sonar technology to track movements of zooplankton in tanks and enclosures, where single species can be isolated and, therefore, easily identified.

In situ tracking of zooplankton swimming behavior using high-speed cinematography and video recording has the potential to provide detailed information on the distribution and range of responses of individual animals within a population. These recording techniques have been used successfully from submersibles or by scuba divers to study large migrants such as antarctic krill (Hamner et al., 1982), medusae (Mills and Goy, 1988) and mysids (Bowers, 1988). With minor technological changes, visual recording could be adaptable to resolve migration behavior of smaller zooplankton (see discussion in Technological Developments, this volume). When compared to complementary population studies of vertical migration, direct in situ observations may help answer questions such as the relationship of individual variability to behavior at the population level.

The ubiquity of diel movement within practically all zooplankton taxonomic groups is impressive. Indeed, it would be far more significant to identify a species or higher taxon that never migrates than to add to the list to those that do migrate. From the variety of migration and distribution patterns of zooplankton and the rate at which they can change one can conclude that diel migration behavior is a form of "evolutionary putty" that can be molded rapidly and precisely to fit each set of biotic and abiotic conditions. In drawing such a conclusion one must assume, however, that behavioral flexibility is not an important component of migration. There is, at this time, inadequate experimental data to support or refute this assumption.

There is clearly a need for research that develops quantitative, testable hypotheses built upon the recognition of the *multiplicity* of factors that shape vertical migration and the *plasticity* of diel behaviors in zooplankton. Among the many critical questions that await resolution are the degree of genetic versus phenotypic control over diel behavior patterns and the importance of ontogenetic changes in migration related behaviors.

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APPENDIX: DISCUSSION AFTER HANEY

L. Hutchings: While we generally view finding food and escaping predation as the ultimate causes of vertical migration, in systems with advection, such as estuaries and oceans, changes in vertical distributions may be made to limit population dispersals or to place eggs in suitable environments.

C. Greene: Ohman et al., (1983) and others have documented relatively rapid changes in zooplankton migration patterns when predation intensity increases. As you mentioned, in most instances we do not know whether such rapid changes are due to genetic shifts or behavioral plasticity. A first step in addressing this question would be to determine whether populations before and after the shift in migration are distinguishable via electrophoretic methods (Weider, 1984). Since electrophoretic results, by themselves, are insufficient to answer the question directly, additional steps should include controlled field or laboratory experiments, similar to those conducted by M. Liebold. Using mesocosms or enclosed in situ water columns, shifts in migration patterns could be monitored upon the inclusion or exclusion of predators and the response time determined. Distinguishing between phenotyic and genetic responses seems critical to our understanding of the evolution and ecology of anti-predator behavior.

J. Haney: It appears that columns and enclosures, so frequently used in community-level experiments, have now come of age for the study of zooplankton migration behavior. Investigators should consider the opportunities to address such questions using the well-designed plankton towers at Plon for freshwater and at Dalhousie for marine organisms.

D. Stearns: Another problem is that when we discuss vertical migration, we tend to assume the entire population is migrating. There is experimental (Joan Laure's work in the 1960's) and field (Bowers, 1988) evidence that only a portion of the population shows vertical movement. If that's true, what does that tell us about the evolution of different behavioral strategies within a population even though they are all exposed to the same selective factors?

M. Ohman: In marine systems, physical factors can readily break up aggregations or merge aggregations from various sources. A single population may be composed of various groups of individuals which have been subjected to different levels of food and predation intensity.

J. Haney: Unfortunately, before we can understand how different migration strategies can develop within a population, we must first identify the behavior patterns within the population. There may be little similarity between migration patterns of the entire population and the migration behavior of individuals. For example, a deep layer of the population that does not change in size with time of day could be the result of many different individual behaviors, including multiple migrations within a diel period and migration cycles of 2 or more days.

W. Hamner: But its very difficult to infer behavioral differences between individuals based on population sampling techniques. We need to develop the ability to track the vertical migrations of single individuals over 24 h. That's never been done in all the thousands of papers on vertical migration in zooplankton.