

The Foraging Ecology of Migratory Shorebirds in Marine Soft-sediment Communities: The Effects of Episodic Predation on Prey Populations¹

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SYNOPSIS. This paper explores the extent to which life histories of infaunal prey have been molded and maintained by predation. It is argued such relationships should be most evident for episodic predation, where the predation is predictable, intense and short-lived. Migratory shorebirds are used herein as model episodic predators. Four stop-over areas in North America, for which experimental data exist, are compared. Evidence exists that Semipalmated Sandpipers in the upper Bay of Fundy maintain the observed life history of their major prey, the amphipod *Corophium volutator*. In southeastern Massachusetts, shorebirds significantly reduce the abundance of their prey but in a frequency-dependent fashion, precluding life history responses of the prey. For Grays Harbor, Washington and Delaware Bay, there is no detectable effect of shorebird predation on the infauna. In three of the four studies, there is no apparent effect of early shorebird migrants in significantly increasing the required stop-over of later migrants by depression of prey densities. The data support the characterization of soft-sediment communities as loosely organized assemblages whose specific constitution is determined more by ecological combining ability than by specific evolutionary responses to associated species.

INTRODUCTION

The effects of predators on soft-sediment communities are highly variable (reviewed most recently by Wilson [1990a]). Characteristics which influence those effects include the density of predators, their feeding rates and their population dynamics. For purposes of this paper, I will divide predation into two categories: chronic predation and episodic predation. Chronic predation refers to the situation where predators are resident for at least most of a year; their feeding rates may vary, *e.g.*, as a function of temperature, but there is always a risk of death from predation for the resident infauna (*e.g.*, Young *et al.*, 1976). Episodic predation occurs when consumers are resident for only a short period of the year. Although episodic predation may have stochastic components (*e.g.*, cownose rays in the Chesapeake Bay [Orth, 1975]), coverage in this paper will be restricted to those situations where the episodes of predation are predictable from year to year.

By dividing predation into these two categories, the evolutionary aspects of com-

munity organization can be examined. The general question posed is: Do infauna respond to predators of particular species or are adaptations general? Prey adaptations are manifold but can be classified into three types: morphological adaptations (*e.g.*, Barnes, 1987), behavioral adaptations (*e.g.*, Woodin, 1982) and life history adaptations (McCall, 1977; Levin, 1984; Wilson, 1989). Obviously, adaptations of one type do not preclude adaptations of other types. This paper will concentrate on life history adaptations.

Various life history responses are possible for organisms exposed to heavy predation. First, species may adopt an opportunistic life history, reproducing as early as possible and dispersing widely to ensure that at least some of one's offspring escape the ravages of predators (Stearns, 1976, 1977). These are adaptations expected under the effects of chronic predation. Alternatively, if episodic predation is simultaneously severe and predictable, the life history response may be quite different. The response may accommodate the episodic predation, for instance by ensuring that the majority of the population is in the least vulnerable stage of the life cycle when predators are present (Wilson, 1989).

In this paper, I will restrict my consid-

¹ From the Symposium on *New Perspectives in Soft-Sediment Ecology* presented at the Annual Meeting of the American Society of Zoologists, 27-30 December 1990, at San Antonio, Texas.

eration to a single taxon of episodic predators, migratory shorebirds (suborder Charadrii of the order Charadriiformes). As explained below, these birds are excellent model episodic predators. Many of these birds migrate from tropical or sub-tropical wintering grounds to breed in the high Arctic. Their arrival on the breeding grounds is constrained to a narrow window of time. If the birds arrive too late, they run the risk of not acquiring a suitable territory (Evans and Pienkowski, 1984), but if they arrive too early, there is the risk of dying due to extreme cold weather or lack of emerging insects. The constraints on arrival time at the breeding grounds constrain arrival and departure times from stop-over areas as well.

To fuel migrations, shorebirds must deposit large quantities of fat; migrations typically occur in a series of long-distance flights between traditional stop-over areas (Myers *et al.*, 1987). This fattening during a limited feeding period requires that these warm-blooded vertebrates feed at prodigious rates. The need to feed rapidly is exacerbated by the high metabolic rates of shorebirds; shorebird rates are higher than predicted on standard scaling curves of avian metabolic rates on body size (Kersten and Piersma, 1987). Shorebirds are known to have significant impacts on prey populations (Kent and Day, 1983; Quammen, 1984; Rafaelli and Milne, 1987; Wilson, 1989). The result of these characteristics is predation which is predictable in duration and intense in effect.

I will examine several studies which have used experimental methods to examine the effects of shorebirds on their infaunal prey. Two questions are posed: is there any evidence that prey have responded evolutionarily to the arrival and departure of episodic predators? and is there any evidence that the abundance of the prey determines the stop-over duration of the predators?

THE UPPER BAY OF FUNDY

The upper Bay of Fundy is a well-known major stop-over area for migratory shorebirds during fall migration (Harrington and Morrison, 1979; Morrison, 1984; Hicklin, 1987). Between late June and early September, over a million shorebirds pass through

the upper Bay. The vast majority are Semipalmated Sandpipers (*Calidris pusilla*) although over 30 other species occur predictably (Hicklin, 1987). During a stop-over of approximately two weeks, the Semipalmated Sandpipers feed rapidly (Boates, 1980; Boates and Smith, 1979; Wilson, 1990*b*), nearly doubling their weight (Hicklin and Smith, 1984) before departing on a non-stop flight of 2,400 km to the coast of Suriname (McNeil and Cadieux, 1972; Richardson, 1979; Morrison, 1984).

Wilson (1989) described a series of predator-exclusion experiments in which shorebirds and total epibenthic predators (shorebirds and bottom-feeding fishes) were excluded. Strong, but counter-intuitive, effects of predators were demonstrated. The exclusion of predators (either shorebirds alone or all epibenthic predators) resulted in a decrease in the total abundance of the dominant prey, adults of the amphipod *Corophium volutator* (Hicklin and Smith, 1979). However, biomass was highest in the exclusion treatments. Analysis of size-frequency distributions suggested that large *C. volutator* which survived in the absence of predation would otherwise have perished by predation. The suggestion that high densities of adult *C. volutator* result in reduced recruitment of juveniles was confirmed by a series of competition experiments which clearly showed that adults at high densities exclude recently released juveniles.

Wilson (1989) suggested that the timing of reproduction in *C. volutator* is constrained by episodic predation. The *C. volutator* which reproduce in the summer, having been born in the spring, do not live through the winter to reproduce again (Gratto *et al.*, 1984; Murdoch *et al.*, 1986; Peer *et al.*, 1986; Wilson, 1988). Therefore, there should be selection on females to reproduce early before the episodic predators arrive. Such timing insures reproduction but has the disadvantage of releasing juveniles into habitats dominated by large numbers of adults, forcing juveniles to disperse widely. On the other hand, delaying reproduction until after the arrival of the episodic predators provides the advantage of releasing juveniles into habitats where adult density is low but the disadvantage of

subjecting the brooding females to predation before brooding is complete. It seems that there is an optimal window of time for reproduction which is maintained by the arrival and departure of episodic predators. Recruitment was greatest when the shorebirds were at their peak population sizes in the Bay (Wilson, 1989). Peer *et al.* (1986) stated that shorebirds arrive at the Bay of Fundy when abundance of *Corophium* is maximal. My data indicate that this statement reverses cause and effect; the effect of predators, by constraining the timing of reproduction and reducing inter-generational competition of the prey, results in maximal *C. volutator* densities.

It is instructive to look at the life history of *C. volutator* in lower reaches of the Bay of Fundy where Gratto *et al.* (1984) showed that *C. volutator* have a single generation per year, rather than the two observed in upper Bay habitats. There are two obvious differences between the two habitats. First, the lower Bay hosts far fewer migratory shorebirds (Lank, 1983). Second, the water in the lower Bay is cooler (Gratto *et al.*, 1984). Either of these differences could translate into the observed life history differences. Temperature differences have been invoked to explain latitudinal variation in life history for other amphipods (Donn and Croker, 1986). A common garden experiment is clearly needed to differentiate between the two effects in the case of *C. volutator*.

The limited available data do not indicate that the effect of early shorebird predation significantly reduces the foraging ability of later-arriving shorebirds. Wilson (1990b) provided data on the foraging rate of Semipalmated Sandpipers from the time of their peak abundance to one week beyond, demonstrating that prey capture rate is not affected by prey density. It was surmised that the constraint limiting intake rate was the rate of digestion.

To summarize, there is evidence that episodic predation contributes to the maintenance of one aspect of the life history of the prey species, *C. volutator*. Data are insufficient with present information to provide an assessment of the importance of episodic predation in promoting the origin of such

life history patterns. Despite the significant impact of shorebirds on the prey populations, later migrants are not disadvantaged by reduction of prey density by earlier migrants.

GRAYS HARBOR, WASHINGTON

For the past three years, I have been performing shorebird exclusion experiments in Grays Harbor, one of two estuaries on the outer coast of Washington. The work is intended as a companion study to my work on the Bay of Fundy. There are several striking similarities between the two systems. During the spring migration, Grays Harbor hosts over a million shorebirds, mainly Western Sandpipers (*Calidris mauri*) with significant numbers of Dunlins (*C. alpina*) and Short-billed Dowitchers (*Limnodromus griseus*) (Herman and Bulger, 1981). Data from the literature indicated that the major prey of the shorebirds were three species of the amphipod genus, *Corophium* (Smith and Mudd, 1976). Thus, this system seems to be ecologically similar to the upper Bay of Fundy but different biogeographically and evolutionarily.

The experimental protocol was the same as used in the upper Bay of Fundy. Two sites (termed East and West) were chosen at the 1.0 m tidal level. At each site, five shorebird exclusion ceilings were erected on 7 April 1988. Each ceiling was made of four wooden stakes arranged in the four corners of a 0.6-m \times 1.2-m rectangle. At that time, a 10-cm diameter core, 10 cm in depth, adjacent to each enclosure was taken to establish initial densities. On 2 May 1988, the experiment was concluded by taking a core, 10 cm in diameter, from the center of each enclosure and a core taken within 1 m of each cage. All samples were sieved on a 500- μ m mesh screen. All organisms retained on the sieve were preserved in formalin and sorted under a dissecting microscope at 12 \times magnification.

The data for the East site are presented in Figure 1. The most common infaunal species is the tanaid crustacean, *Leptocheilia dubia*. However, there is no significant difference between any of the three treatments (the 10 April control (Initial), the May control (Control) and the shorebird exclusion

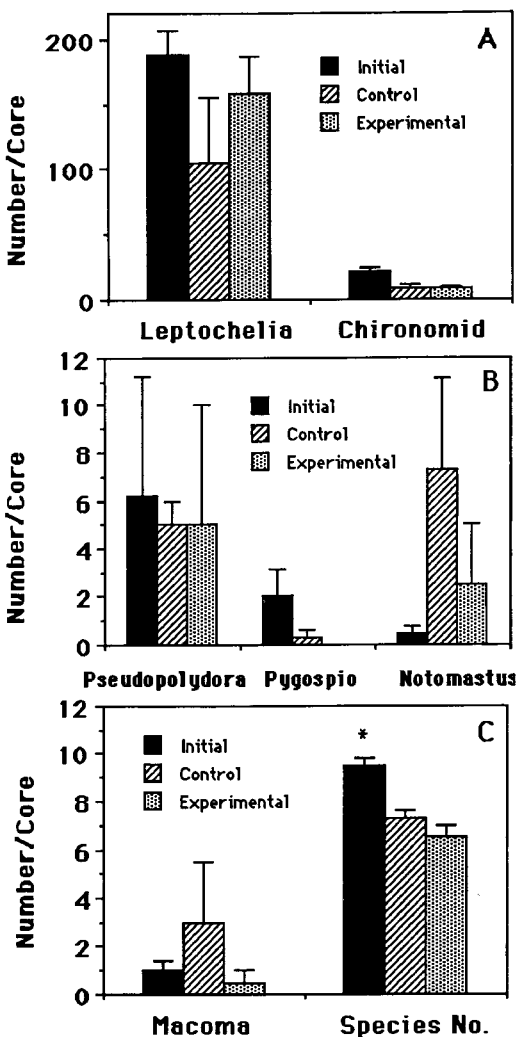


FIG. 1. The abundances of common species and species richness for the East Site at Bottle Beach, Grays Harbor, Washington. Initial refers to samples taken on 12 April 1988 before the arrival of migratory shorebirds; Control refers to samples from unmanipulated areas taken on 10 May 1988 after the shorebird migration; Experimental refers to samples taken from shorebird exclusion cages on 10 May 1988. All means were based on five replicate cores, each 0.008 m² in area. Asterisks above a column denote means that are significantly different from other means ($P < 0.05$).

treatment (Experimental) (Fig. 1A). Treatment abundances for chironomid insect larvae did not vary (Fig. 1A). There is no significant difference in the treatment abundances for the spionid polychaetes, *Pseudopolydora kempfi* and *Pygospio ele-*

gans, or the capitellid polychaete, *Notomastus* sp. (Fig. 1B). No statistical difference in the treatment abundances of the bivalve, *Macoma balthica*, was found (Fig. 1C). There was a significant drop in the number of species found per core between April and May (Fig. 1C) both in the presence and absence of shorebirds. No species disappeared over the time interval.

For the West site, relative abundances of the species differed from the East site but the results of shorebird exclusion were qualitatively similar. There were no significant treatment differences for the crustaceans, *Leptochelia dubia* or *Cumella vulgaris*, or chironomid larvae (Fig 2A). For *Corophium spiniornis*, there was a significant decrease in abundance between April and both of the May treatments (Control and Experimental). I do not present size-frequency data for *C. spiniornis* because of the relatively small numbers of complete individuals retained. However, no juveniles were found, indicating that release of juveniles was not occurring during late April.

The responses of the three spionid polychaetes were varied. No significant differences among treatments were seen for *Pseudopolydora kempfi* (Fig. 2B). For *Pygospio elegans*, the Control abundances were inexplicably higher than either the Initial or Experimental abundances (Fig. 2B). For *Streblospio benedicti*, there was a significant increase in density between April and May which was not associated with the exclusion of shorebirds (Fig. 2B).

Other co-occurring infauna at the West site showed no differences among treatments (the bivalve *Macoma balthica* and the polychaete *Tharyx multifilis*) (Fig. 2C). A significant increase in the number of species found per core occurred between April and May, independent of shorebird exclusion (Fig. 2C).

The results of this experiment indicate that the presumed similarity of the Bay of Fundy to Grays Harbor is superficial. Despite the fact that similar numbers of shorebirds pass through each region, the effects of these episodic predators on the infauna are quite different. In the Bay of Fundy, shorebirds (notably Semipalmated Sandpipers) fundamentally affect the abun-

dance and demography of a single species, *Corophium volutator*. In Grays Harbor, there are no consistent strong effects of shorebirds (notably Western Sandpipers) on any of the infauna. Observations of foraging Western Sandpipers indicated that they were successfully capturing prey but their tendency to feed in areas with a shallow covering of water made field identification of their prey difficult. However, gut analyses from Washington and Alaska indicate that major prey are *Corophium* spp., *Macoma balthica* and various polychaetes (Smith and Mudd, 1976; Senner, 1979; Senner *et al.* 1989).

Despite the similar size and metabolic rates of Western and Semipalmated Sandpipers, the difference in the intensity of their predation may involve differences in migratory routes. Unlike the transoceanic flight of the Semipalmated Sandpipers, Westerns have a shorter flight to fuel. It is known that the Copper River Delta in south-central Alaska is a stop-over for virtually all of the western Nearctic migrants (Isleib, 1979; Senner, 1979; Senner *et al.*, 1981), a distance of 1,500 km from Grays Harbor. Many shorebirds stop at Boundary Bay on the south end of Vancouver Island (Butler *et al.*, 1987; Butler and Kaiser, 1988), 250 km north of Grays Harbor. There may be other unrecognized stop-overs along the coast of Vancouver Island and southeastern Alaska. The stop-over duration at Grays Harbor for Western Sandpipers is typically only a few days for most migrants (Herman and Bulger, 1981; Wilson, unpublished data). Thus, Westerns spend a relatively short amount of time foraging and apparently do not need to accumulate massive fat reserves to fuel the next leg of their journey. There seems to be no strong linkage between shorebirds and their prey; the shorebirds seemingly can fatten sufficiently to continue on their journey. Prey are not reduced enough by early migrants to reduce the foraging success of later migrants. Concomitantly, the predation rate does not seem to be strong enough to produce any sort of life history response on the part of the prey.

PLYMOUTH BAY, MASSACHUSETTS

In southeastern Massachusetts, a relatively small number of shorebirds (mainly

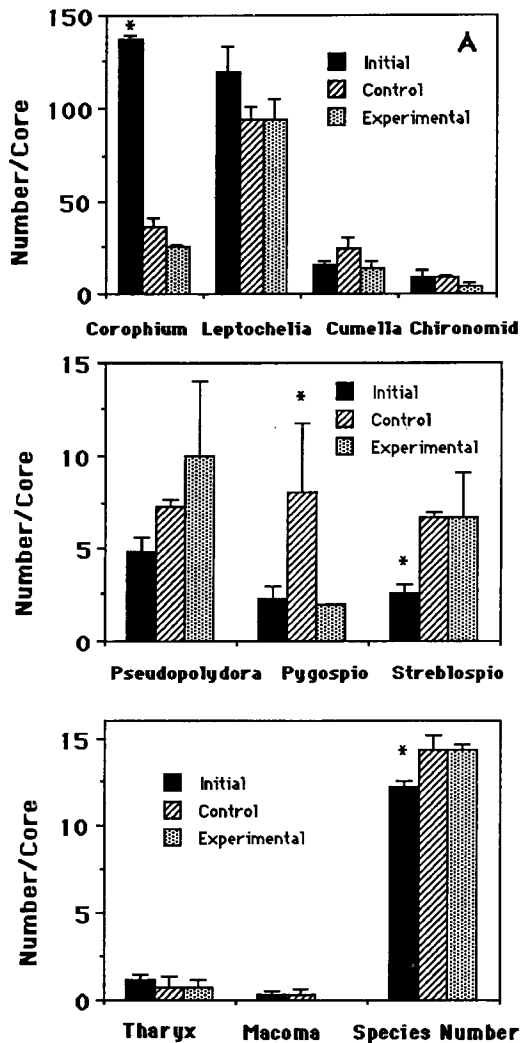


FIG. 2. The abundances of common species and species richness for the West Site at Bottle Beach, Grays Harbor, Washington. Initial refers to samples taken on 12 April 1988 before the arrival of migratory shorebirds; Control refers to samples from unmanipulated areas taken on 10 May 1988 after the shorebird migration; Experimental refers to samples taken from shorebird exclusion cages on 10 May 1988. All means were based on five replicate cores, each 0.008 m² in area. Asterisks above a column denote means that are significantly different from other means ($P < 0.05$).

Semipalmated Sandpipers and Short-billed Dowitchers) stop-over during the fall migration. Schneider (1978) described a series of exclusion experiments in which he documented what he termed "equalisation of prey numbers," an effect which obtains

when predators take abundant prey in greater proportion than their relative abundance while rare prey are taken in lower proportion than expected by their relative abundance. The prey taken preferentially included the polychaetes *Clymenella torquata*, *Nereis virens*, *N. arenaceodentata*; the amphipods *Acanthohaustorius millsi* and *Trichophoxus epistomus*; and the bivalve *Tellina agilis*. Mortality rates of the abundant organisms ranged between 67–84%, although there was variation in the dominance rank of the various species.

It seems unlikely that the life history patterns of any of these species can be understood in terms of episodic predation. Although shorebirds represent a potent mortality source, the risk depends wholly on the relative abundance of each species at a particular site. Shorebirds on Plymouth Bay flats seem to specialize locally on the invertebrates that are the most abundant. Only species which are consistently dominant would be expected to respond evolutionarily to the arrival of episodic predators. The flats here are also small; it seems likely that dispersal to proximate areas which do not experience heavy shorebird use would dilute any localized adaptations. Furthermore, the reproduction of *Nereis virens* takes place in May (Snow and Marsden, 1974; Creaser and Clifford, 1982; Wilson and Ruff, 1988); the reproduction of *N. arenaceodentata* from May until September (Pettibone, 1963) and the reproduction of *Clymenella torquata* in the spring (Rowe and Tyler, 1969).

Schneider and Harrington (1981) argued that depletion of prey may determine the duration of stop-over of shorebirds in Plymouth Bay. Although the factors determining departure of shorebirds from a stop-over area are contentious, Schneider and Harrington's data are consistent with this hypothesis. However, this site hosts fewer than 4,000 shorebirds; even if later migrants are forced to stop-over for longer periods of time, this may affect only a small percentage of the total population.

DELAWARE BAY

During May, Delaware Bay is host to spectacular concentrations of shorebirds

(Myers *et al.*, 1987). It is estimated that 90% of the Nearctic population of Red Knots (*Calidris canutus*) pass through Delaware Bay en route to their tundra breeding grounds (Harrington *et al.*, 1988). Other abundant migrants include Semipalmated Sandpipers, Semipalmated Plovers (*Charadrius semipalmatus*) and Ruddy Turnstones (*Arenaria interpres*). This period coincides with the onshore breeding migration of great numbers of horseshoe crabs (*Limulus polyphemus*) (Shuster and Botton, 1985). The energy-rich eggs (4 mm in diameter) form the major food item for the shorebirds; the eggs sometimes wash up in windrows at the high tide level. Botton (1984) examined the effects of both shorebirds and fish on the infauna in southern New Jersey shores of Delaware Bay where greatest numbers of both shorebirds and horseshoe crabs occur. The infauna is dominated by the small venerid clam, *Gemma gemma*. Schneider (1978) claimed that most *G. gemma* pass through shorebird guts undigested (although small bivalves comprise a portion of the diets of many shorebirds). Botton (1984) could document no significant effect of shorebirds on the infauna. There is clearly a superabundance of *Limulus* eggs in Delaware Bay (B. Harrington, personal communication).

The Delaware Bay system seems to represent yet another example of a loosely structured predatory-prey system. The widespread *L. polyphemus* breed from Maine to Georgia and range broadly over the continental shelf during the remainder of the year, precluding localized adaptation (Botton and Loveland, 1987). Delaware Bay is a particularly important site for *L. polyphemus* mating but the success of the species does not solely depend on the reproductive success in Delaware Bay. Thus, it is unlikely that this "prey" species is influenced by the localized episodic predation events.

On the other hand, there is no evidence available to suggest that prey depletion is occurring at Delaware Bay. Earlier migrants seem to spend more time at Delaware Bay than later migrants (Harrington, personal communication). The average stop-over at the site is about 10 days.

PREDATION AND EVOLUTION OF PREY LIFE HISTORIES

The preceding analyses have explored the general phenomenon of prey responses to predation, particularly addressing the tightness of community organization of soft-sediment communities. I examine whether prey life histories are generalized responses or rather are responses to especially potent sources of mortality. Episodic predation was chosen as the cornerstone of my analysis. If episodic predation is both predictable and potent, then it should be possible to see evidence of the molding of prey life histories to minimize the impact of such predation. I submit that the most likely place to see a direct relationship between predation and the evolutionary response of the prey is under such conditions.

The effects of episodic predators was examined at four major stop-over areas for shorebirds in North America. In two instances (Delaware Bay, Grays Harbor), no evidence can be marshalled to indicate that episodic predation has a significant impact on prey abundance. Hence, an evolutionary response of prey life history is not expected. In both of these cases, there is no evidence that early migrants depress abundance of prey such that later migrants are forced to tarry longer in order to acquire the necessary fuel reserves to continue their migration.

For southeastern Massachusetts, significant predation was seen but was not predictably observed on a single species. Rather, the most abundant species locally had to endure the heaviest predation. However, for proximate areas where a particular species was locally rare, it benefitted from its rarity. Given the relatively small area of the study site, the patchiness of prey distribution and the potentially great dispersal of many of the prey species, it is unlikely that localized life history adaptations would be seen. In fact, published accounts of the major prey species indicate that most have reproduced by the time the shorebirds have arrived. From the point of view of the shorebirds, Schneider and Harrington (1981) cite evidence that later migrants linger longer than earlier migrants, implying that early migrants significantly depress the abundance of infauna.

The best evidence for an interaction of episodic predation and prey life history comes from the upper Bay of Fundy where size-selective predation by migratory shorebirds (and, to a lesser degree, epibenthic fish) ameliorates competition between generations of the dominant prey species, *Corophium volutator*. As argued elsewhere (Wilson, 1989), there is directional selection on the timing of reproduction for this prey species. Early reproduction results in nearly certain release of juveniles but into populations with high numbers of adults which effectively exclude juveniles. Late reproduction results in release of juveniles into populations where the size-selective predators have removed many of the adults but carries the risk of death to the parent before brooding is complete.

Biogeographic evidence is intriguing but not conclusive. It should be pointed out that not all of the upper Bay of Fundy flats receive equal shorebird use. Morrison (1984) indicates that 90% of the shorebirds occur at only five sites. However, these sites are all dominated by *Corophium volutator*. In the absence of transplant or common garden experiments to determine the effect of temperature on life history, nothing can be inferred about the evolutionary origin of the life history pattern of *C. volutator*. However, in the upper Bay of Fundy, it seems inescapable that the maintenance of the life history is driven, at least in part, by episodic predation.

The analyses presented here seem to corroborate the inferences drawn by Wilson (1990a) that the organization of soft-sediment communities is characterized by weak interspecific interactions. The assemblage of infauna at a given site may be more a function of ecological combining ability. That is, every infaunal species has a particular suite of life history characteristics that adapt it for a given competitive and predatory milieu. There is a relative paucity of studies which have documented biogeographic patterns of life history within a single species that can be related to differences in ecological characteristics. One outstanding exception in this regard is Gilman's (1979) study of *Macoma balthica* where he documented a tendency toward earlier

reproduction in Chesapeake Bay populations than in Woods Hole or New Brunswick populations. These differences were independent of temperature effects as they were consistently seen when members of the different populations were maintained under the same environmental conditions. It is not clear if the lack of additional examples of life history variation is due to a lack of investigation or a lack of the phenomenon. The results of my survey of episodic predation suggest that there may be a dearth of examples to be found. The characterization of infaunal communities as exceptionally loosely organized communities whose members may be determined by their ecological combining ability should be the working paradigm.

ACKNOWLEDGMENTS

The research at Grays Harbor was supported by a faculty grant from the University of Washington GSRF Program. I am grateful for the critical comments of Betsy Brown, Ray Highsmith and Les Watling which substantively improved the manuscript.

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