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Polinices Predation Patterns and Mercenaria Morphology Models

Abstract

DeAngelis et al. (1985) have described a model of the evolutionary response of bivalve prey to size-selective naticid snail predation. The model analyzed "the allocation of bivalve energy among reproduction, overall growth in size, and supplementary growth in shell thickness" (p. 818). Using parameter values for *Polinices duplicatus* as the predator and *Mercenaria mercenaria* as the prey, the model predicted three optimal strategies for bivalves faced with naticid predation: (1) delayed reproduction with energy diverted into rapid growth in order to reach a size refuge; (2) early reproduction, possibly with some extra shell thickness; and (3) greatly increased shell thickness for deterring predator attacks. This model and an earlier one (DeAngelis et al. 1984) are elaborations on a general qualitative model for bivalve prey (Seed and Brown 1978). [excerpt]

Keywords

bivalves, predation patterns, morphology models

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NOTES AND COMMENTS

POLINICES PREDATION PATTERNS AND *MERCENARIA*
MORPHOLOGY MODELS

DeAngelis et al. (1985) have described a model of the evolutionary response of bivalve prey to size-selective naticid snail predation. The model analyzed "the allocation of bivalve energy among reproduction, overall growth in size, and supplementary growth in shell thickness" (p. 818). Using parameter values for *Polinices duplicatus* as the predator and *Mercenaria mercenaria* as the prey, the model predicted three optimal strategies for bivalves faced with naticid predation: (1) delayed reproduction with energy diverted into rapid growth in order to reach a size refuge; (2) early reproduction, possibly with some extra shell thickness; and (3) greatly increased shell thickness for deterring predator attacks. This model and an earlier one (DeAngelis et al. 1984) are elaborations on a general qualitative model for bivalve prey (Seed and Brown 1978).

DeAngelis et al. (1985, p. 838) referred to my work (Commito 1982) on the response of the bivalves *Mya arenaria* and *Macoma balthica* to predation by the naticid *Lunatia heros* at Federal Harbor, Maine. Compared with *Macoma balthica*, *Mya arenaria* delays reproduction and grows faster until it reaches a size refuge from naticid predation. Because *Macoma balthica* is too small as an adult to ever reach such a refuge, its strategy is to reproduce early. Although DeAngelis et al. (1985) were correct in their assertion that *Mya arenaria* and *Macoma balthica* appear to fit model strategies 1 and 2, respectively, the main point of my paper was not that the two bivalves differ in their life history strategies, but that they differ so little. In fact, *Macoma balthica* has evolved in a way that the model could not have predicted. This species violates the model's fixed allometric relationship between overall body size and siphon length. Despite its smaller size, slower growth, and thinner shell, *Macoma balthica* experiences higher survival rates than does *Mya arenaria* at Federal Harbor (76.3% vs. 3.5% per year for the first 5 years of life). I suggested that *Macoma balthica* may be able to reach a depth refuge from shallow-burrowing naticid predators because of its extremely long siphons. Whereas *Mya arenaria* lives relatively close to the sediment-water interface (siphon length \approx shell length), small *Macoma balthica* individuals may be found deep within the sediment (siphon length $\approx 5 \times$ shell length). Blundon

and Kennedy (1982a,b) showed that *Macoma balthica* lives deeper in the sediment than similarly sized *Mya arenaria* individuals in Chesapeake Bay. Their laboratory tests with *Mya arenaria* and blue crabs (*Callinectes sapidus*) demonstrated clearly that predation is much more intense on individuals inhabiting shallow areas than on those inhabiting deep ones.

The DeAngelis et al. (1985) model failed to take into account that, for many infaunal bivalves, shell length correlates positively with the depth of life position within the sediment. Any reduction in predation mortality associated with large body size may result from the bivalve's attaining a depth refuge from predation. By altering the allometric relationship between overall body size and siphon length, bivalves have opened up an alternative adaptive avenue to increased fitness. The DeAngelis et al. (1985) model made the unrealistic assumption that the only morphological adaptations for defense available to bivalves are growing large or producing a thick shell. The model's *Mercenaria mercenaria* may possess a large body size and thick shell because its short siphons constrain it to a shallow life position. Many infaunal bivalve species (such as *Macoma balthica* and other tellinids) employ a different strategy. They can afford small body sizes and thin shells because their long siphons provide them with the opportunity to attain spatial refuges from predators. However, the high surface-to-volume ratio of long siphons and the regeneration necessary after tip removal by non-naticid predators (Trevallion et al. 1970; Peterson and Quammen 1982; Woodin 1984) may confer on long siphons a high metabolic cost.

The model of DeAngelis et al. (1985) ignored other types of prey defense as well. Shell ornamentation in the form of ridges, knobs, spines, and other protuberances may make handling and drilling by naticids more difficult (Vermeij 1978). Such ornamentation may be energetically cheaper to produce than a larger body or a thicker shell. The model also ignores chemical defense mechanisms. Many sessile and slow-moving benthic animals contain toxic substances that make them unpalatable to predators (Bakus and Green 1974; Bakus 1981). The production or sequestering of these compounds may be energetically less costly than increased body growth and shell production. Finally, behavioral responses to predators are not incorporated into the model. Bivalves may swim or burrow away quickly when under attack (Peterson et al. 1982). All of the evolutionary responses described here (behavioral escapes, chemical defenses, shell ornamentation, shell thickening, large overall body size) are probably more important for bivalves with short siphons than for bivalves having long siphons and living in deeper habitats because the latter are protected by their greater depth in the sediment.

The probability of closely linked coevolution between bivalves and naticids may be low. Bivalves are exposed to many different predators, and naticids can consume a variety of prey types. However, the model of DeAngelis et al. (1985) remains an interesting attempt to predict the evolutionary responses of bivalves to naticid predation. The model was improved over its earlier version (DeAngelis et al. 1984) by allowing nonallometric shell thickening. It will gain further realism and utility when behavioral, chemical, and additional morphological adaptations are also included.

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