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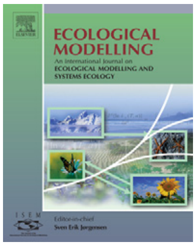

Conditions for coexistence of freshwater mussel species via partitioning of fish host resources

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ABSTRACT

Riverine freshwater mussel species can be found in highly diverse communities where many similar species coexist. Mussel species potentially compete for food and space as adults, and for fish host resources during the larval (glochidial) stage. Resource partitioning at the larval stage may promote coexistence. A model of resource utilization was developed for two mussel species and analyzed to determine conditions for coexistence. Mussel species were predicted to coexist when they differed in terms of their success in contacting different fish host species; very similar strategies offered limited possibilities for coexistence. Differences in the mussel species' maximum infestation loads on the fish hosts that coincided with differences in their fish host contact success promoted coexistence. Mussel species with a given set of trade-offs in fish host use were predicted to coexist only for a subset of relative fish host abundances, so a shift in relative fish host abundances could result in the loss of a mussel species. An understanding of the conditions for freshwater mussel species coexistence can help explain high mussel diversity in rivers and guide ongoing conservation activities.

1. Introduction

Communities of freshwater mussels of the family Unionidae in many North American rivers support high diversities of similar species over long periods of time. For example, some rivers consistently support 20–40 freshwater mussel species (e.g., Strayer, 1980; Ahlstedt, 1986). These species are similar in terms of their use of food and habitat resources (Coker et al., 1921; Fuller, 1980; Strayer, 1981; Bronmark and Malmqvist, 1982; Hanson et al., 1988; Strayer, 1993). Virtually all North American freshwater mussel larvae (glochidia) are obligate parasites on fish for a period of weeks to months during recruitment (Fuller, 1974). Most mussel communities are thought to be limited at recruitment (Young and Williams, 1984; Haag and Warren, 1998), so populations may be regulated by the number of new post-glochidial recruits supplied to the site, rather than by interactions between adults (Grosberg and Levitan, 1992; Chesson, 1998). It is possible that mussel species compete for fish hosts (Bauer, 2001). Larvae of a particular mussel species can only develop successfully on a subset of the fish species in a river (Bauer and Vogel, 1987; Waller and Holland-Bartels, 1988). Most species are specialists, using one or a few host fish species, although some generalists may use a dozen hosts or more (Strayer et al., 2004). Ecologically similar species, such as these, are expected to compete for the resources that most

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limit population growth. Because it is unlikely that two species will be perfectly balanced in their abilities to use resources, the stronger competitor is expected to outcompete the weaker competitor and force its exclusion (Hardin, 1960).

Coexistence among freshwater mussels that overlap on fish hosts may be facilitated by the partitioning of fish host resources used during recruitment (Fuller, 1980). Resource partitioning promotes species coexistence because species differ from each other in at least one ecological characteristic that allows them to utilize different portions of the resource spectrum (Schoener, 1974). Early theoretical work by MacArthur and Levins (1967) and May (1974) showed that species in competition for a single, continuously-distributed resource could coexist only if their resource utilization differed by a limiting similarity. However, Abrams (1983) found that models with competition in different dimensions or with alternate utilization curves lead to alternate limits to similarity. In the case of multiple substitutable resources, such as species of fish hosts for mussels, a general condition for coexistence is that each competing species must remove at a higher rate the resource that contributes more to its own growth rate (Leon and Tumpson, 1975; Tilman, 1982; Abrams, 1987a,b). The importance of trade-offs in resource use among species has been emphasized recently as a mechanism promoting coexistence in plant communities (Silvertown, 2004). Resource partitioning during the glochidial stage may determine species coexistence for freshwater mussels. However, to date this hypothesis has not been addressed quantitatively.

In this paper, mathematical conditions for coexistence via resource partitioning of host fish were derived for two species of freshwater mussels. A model of resource utilization was developed for the mussel species, in which larval and adult stages were assumed to occupy different niches. Adults of each species were assumed to overlap with each other in terms of food and habitat use and larvae were assumed to overlap in their use of two species of fish hosts. Invasibility analysis was used to determine conditions for coexistence, and the effects of host contact success, carrying capacities (in this case, the maximum glochidial infestation rates per fish), and fish host densities on coexistence were examined. An understanding of the conditions for coexistence of freshwater mussel species may foster an explanation of the factors promoting the high mussel diversity found in some rivers, and may also guide ongoing conservation activities, such as mussel transplants and population augmentations (e.g., Ahlstedt, 1979; Cope and Waller, 1995; Biggins and Butler, 2000). Conservation activities and efforts are crucial because over seventy percent of North American freshwater mussel species are in decline, threatened, or extinct (Williams et al., 1992) and the fauna is undergoing extinctions in the “kilo-death” range (Nott et al., 1995).

2. Methods

2.1. *A model of competition between two mussel species*

The two competing mussel populations, *i* and *j*, are represented by difference equations with yearly time steps. Consider mussel population *j*. Its adult population size at the end of the breeding season of year $t+1$, $N_j(t+1)$, can be represented by two terms, which are functions of the population size in the preceding year; survivors from the preceding year, and new recruits. For the case of two competing mussel species, the adult survivorship is a function of the densities of the two species;

$$N_j(t+1) = \frac{S_j N_j(t)}{1 + \alpha_{ij} N_i(t) + \alpha_{jj} N_j(t)} \tag{1}$$

where α_{ij} and α_{jj} are coefficients of competition for space and food.

The expression for recruitment at time $t+1$ is more complex. Assume that there are two fish species that can each be utilized by both mussel species, and that the number of fish of each species remains roughly constant at F_1 and F_2 during the mussel breeding period. Also assume that the two host fish species have maximum possible infestation loads for glochidia of species *j* of K_{j1} and K_{j2} and for species *i* of K_{i1} and K_{i2}. Then, in the limit of very large production of glochidia by species *j* alone, all of the available spaces on the fish, $K_{j1}F_1 + K_{j2}F_2$, should be occupied by glochidia. Assume that the probability of a given glochidia of mussel species *j* finding a fish is

$$r_j = c_{j1}K_{j1}F_1 + c_{j2}K_{j2}F_2, \tag{2}$$

where c_{j1} and c_{j2} represent the ability of mussel species *j* to contact fish hosts 1 and 2, respectively. Then, when there are two competing mussel species, a possible representation for the number of glochidia of species *j* that attach to fish is

$$\frac{f_j r_j N_j(t)}{1 + [r_j/\{[K_{j1}F_1/\{(c_{i1}/c_{j1})f_i N_i(t) + f_j N_j(t)\}] + [K_{j2}F_2/\{(c_{i2}/c_{j2})f_i N_i(t) + f_j N_j(t)\}]\}]} \tag{3}$$

In this expression, f_i and f_j are the fecundities of the individual mussels of species *i* and *j*, and $N_j(t)$ represents the number of adults at the start of reproduction. It is assumed that reproduction occurs before the losses of adults due to mortality. This expression reduces to $K_{j1}F_1 + K_{j2}F_2$ in the limit of very high glochidia production by mussel species *j* (assuming species *i* is not highly productive). In the limit of very small glochidia production by mussel species *j*, again in the absence of mussel species *i*, the expression reduces to $f_j r_j N_j(t)$. These limiting cases are reasonable. The effects of competition also seem to be incorporated in a reasonable way, as, in the case of high glochidia production by both species, the fraction of sites occupied by species *j* is reduced by the factor

$$\frac{f_j N_j(t)}{(c_{i1}/c_{j1}) f_i N_i(t) + f_j N_j(t)}, \tag{4}$$