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Relative importance of predation and intraspecific competition in regulating growth and survival of juveniles of the soft-shell clam, *Mya arenaria* L., at several spatial scales

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Abstract

Predation appears to be the single most important biotic factor regulating populations of bivalves in estuarine and coastal soft sediments. However, the relative roles of predation and intraspecific competition are rarely investigated simultaneously over different spatial scales, making generalities about these mechanisms difficult. Using juveniles of the soft-shell clam, *Mya arenaria* (initial mean shell length [SL] ± 95% CI = 12.4 ± 0.13 mm), I tested the interactive effects of predator deterrence and intraspecific density (660 vs. 1320 individuals m^{-2}) on growth and survival responses over a 185-day period from May to November 2003 at spatial scales that spanned four orders of magnitude: embayments, sites within embayments, tidal gradients, and blocks that were 10,000's, 1000's, 100's, and 5 m apart, respectively. Replicate field experiments were conducted from May to November 2003 at the upper and lower tidal heights at each of two intertidal mud flats (sites) within each of two embayments (Passamaquoddy Bay [PB] and Cobscook Bay [CB]) in eastern Maine.

Mean survival, relative growth, and the abundance of wild recruits each varied significantly over all spatial scales. Predation was the most important factor affecting clam survival, explaining 45% of the total variability, whereas embayment, sites within embayments, tidal gradient, and intraspecific density collectively accounted for less than 10% of the variation. At all four intertidal sites, clam survival in experimental units designed to deter predators averaged 72%, but the degree of enhancement varied between embayments (PB = 61%; CB = 267%). Average survival rate was higher (by 12–16%), but growth was slower (by ca. 50%) in upper vs. lower intertidal blocks; however, the patterns differed for both variables between sites within each embayment. The effect of increasing intraspecific clam density was to lower survival by ca. 17% (56% [660 m^{-2}] vs. 48% [1320 m^{-2}]) in both embayments, but growth was unaffected. Overall, clams doubled in SL, although mean relative growth was 15% greater in CB than PB. Tidal gradient, sites within embayments, and blocks were the three most important factors explaining 35%, 19%, and 22% of total variation in relative clam growth, respectively. In Maine and the northeast US, juveniles of *Mya* reach their highest abundance above mean low tide levels. Experimental evidence presented here suggests that differential predation along the tidal gradient is the dominant factor controlling clam abundance and distribution patterns in the intertidal zone.

Keywords: Bivalve; Growth; Intraspecific competition; Maine; *Mya arenaria*; Predation; Spatial scale; Survival; Tidal gradient

1. Introduction

Over the past four decades, marine ecologists investigating the regulation of invertebrate populations within low-energy, shallow-water and intertidal soft-

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bottom communities have paid considerable attention to the role of predation and competition (Virnstein, 1977; Peterson, 1982a,b; Wilson, 1990; Thrush, 1999; Quijón and Snelgrove, 2005). Notwithstanding the current debate regarding the importance of pre- and post-settlement interactions in structuring these communities (Caley et al., 1996; Fraschetti et al., 2003), the present model for established residents of unvegetated soft sediments posits that predation (whether infaunal, epifaunal, partial, or complete) is more important in controlling the distribution and abundance of residents than competition for food or space (Micheli, 1997). This idea, first reviewed by Peterson (1979) and expanded by Commito and Ambrose (1985) and Ólafsson et al. (1994), has been supported generally by several experimental field investigations involving burrowing bivalves in the order Veneroida (Peterson, 1982b; Black and Peterson, 1988; Richards et al., 1999). The relative importance of predation is inferred from other studies where predator abundance primarily had a negative effect on prey abundance of taxa as diverse as polychaetes (Desroy et al., 1998; Beukema et al., 2000), amphipods (Hilton et al., 2002), and gastropods (Ray and Stoner, 1995). However, effects of predation and other biotic factors on population growth and recruitment may vary over different spatial scales (e.g., between sites outside different estuaries or within the same estuary, or along tidal gradients) complicating interpretations of how populations respond to these agents (Peterson and Beal, 1989; Micheli, 1996; Legendre et al., 1997; Constable, 1999; Seitz and Lipcius, 2001; Thrush et al., 2000).

Generalizations about population processes in marine soft-sediments largely have been developed based on a limited number of field sites and/or sampling times, and specific results from field experiments may vary depending on the spatial scale that trials are carried out (sensu Thrush et al., 2000). At least three experimental approaches have been adopted by benthic ecologists to examine how predation and other mechanisms vary over different spatial scales. One method is to manipulate the size of experimental units, prey patches, or habitats and examine how processes change across different levels of the factor (Whitlatch et al., 1997; Fernandes et al., 1999). Another is to conduct similar experiments at the same time in two or more ecosystems differing in scale (Seitz and Lipcius, 2001). A third approach, used here, is to establish the same experiment at two or more geographically distinct sites or different habitats to examine interactions between local- and broader-scale processes (Thrush et al., 2000).

Sedentary, intertidal marine bivalves afford a unique tool to test how spatial scales affect ecological processes because their densities are relatively easy to manipulate without large handling mortalities, predator exclusion is relatively straightforward, growth and survival rates of marked individuals are easily measured, and their effect on recruitment of con- and/or heterospecifics can be measured. The soft-shell clam, *Mya arenaria*, is a suspension-feeding bivalve that occurs subtidally and intertidally in the western Atlantic, from North Carolina to Newfoundland (Abbott, 1974). In the northeast U.S. and Canadian Maritimes, its greatest abundance, and nearly 100% of its commercial exploitation, occurs in the intertidal zone (Wallace, 1997). *Mya* is iteroparous, and its growth is size-, site-, and habitat-dependent (Brousseau, 1978, 1979). In Maine, USA, *Mya* grows seasonally from April to November when seawater temperatures are above 5 °C (Beal et al., 2001). Because annual growth rates are highest among juveniles (<12 mm shell length, SL), and these small individuals are more susceptible to epibenthic and infaunal predators than larger conspecifics, simultaneous field manipulations of 0-year class individuals across several locations should permit strong tests about the role of specific ecological processes.

The purpose of this manipulative field study was to examine over a 185-day growing season (May to November) the interactive effects of predation and intraspecific competition on growth and survival of juveniles of *Mya* over four spatial scales ranging from 0.05 km to 10's of km. The field experiment was conducted along a tidal gradient at each of two intertidal sites in lower Passamaquoddy Bay and upper Cobscook Bay in eastern Maine. Based on previous field trials with soft-shell clam juveniles (Beal, 1994; Beal et al., 2001), I expected that at every site survival would be affected most by predation. Further, I expected that predation intensity would be greatest in the lower intertidal zone because these areas are exposed to higher numbers of waterborne predators than in the upper intertidal zone. In addition, because intertidal bivalve growth typically is a function of time of tidal inundation (Peterson and Black, 1987), I anticipated that juvenile clams growing near the lower intertidal zone would be significantly larger than those growing near the upper intertidal zone at the end of the experiment. Density-dependent reduction in growth was anticipated only where resources were potentially in short supply (Weins, 1977); that is, at high shore levels where suspended food is temporally limited relative to lower on the shore.

2. Methods

2.1. Experimental animals

Juvenile soft-shell clams, *M. arenaria*, used in this study were hatchery-reared individuals obtained from the Beals Island Regional Shellfish Hatchery of the Downeast