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# Hierarchical spatial structure in soft-bottom mussel beds

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**Abstract**

Mussels (*Mytilus edulis* L.) are unusual because they thrive in both rocky shore and soft-bottom habitats. Despite their ecological and economic importance, little is known about their spatial structure. Mussels do not generally recruit to bare soft substrate because larvae and postlarvae cannot attach to a bottom of small sediment particles. They attach to hard objects on the sediment surface (especially other mussels), so soft-bottom mussel beds may be spatially organized in ways that are fundamentally different from those on rocky shores. The purpose of our study was to characterize the scales of spatial variability for several mussel abundance parameters in soft-bottom, intertidal *M. edulis* beds in coastal Maine. We used a random factor nested-ANOVA design of 200 $cm^2$ Cores within 1 $m^2$ Quadrats within 6 m Transects within Positions within bed Sites along 70 km (euclidean distance) of the Maine coast. Based on the literature and our field observations, we hypothesized that Sites and Positions account for most of the spatial variance in soft-botttom mussel beds. We rejected this hypothesis. Sites and Positions were not important in explaining variation in total mussel density, density of new recruits, or density of larger mussels. Although most of the variance in surface silt–clay fraction did occur at these levels, most mussel variation occurred at smaller spatial scales, specifically at the Quadrat scale for new recruits and total mussels and at the Transect scale for larger mussels. Variance in mussel parameters was not closely linked to the silt–clay fraction of surface sediment or to Site rankings of wind exposure and tidal flow. Variance in total mussel density was due primarily to variance in recruitment. No single scale explained more than about half the mussel variance, and no single scale was best at explaining all the mussel parameters. Greater knowledge about mussel bed spatial variability would be useful because it can help direct scale-dependent sampling regimes, field experiments, and coastal management practices.


*Keywords:* Ecosystem engineer; Hierarchical spatial structure; Maine; Mussel bed; *Mytilus*; Soft-bottom

## 1. Introduction

Mussel beds are ubiquitous coastal features in soft-bottom and rocky shore habitats around the world. Beds of the blue mussel, *Mytilus edulis* L., are common in both habitats and have enormous ecological and economic significance (see Commito and Dankers, 2001; Commito et al., 2005 for reviews). Despite their importance, surprisingly little is known about their spatial structure. Much of that spatial information comes from the rocky shore, where mussels can potentially recruit onto any bare hard substrate. However, mussels do not generally recruit to bare soft substrate because larvae and postlarvae cannot attach to a bottom of sediment particles that are small and subject to bedload transport. Instead, they attach to hard objects on the sediment surface, particularly live mussels and empty

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valves (Dankers et al., 2001). Thus, soft-bottom mussel beds may be spatially organized in ways that are fundamentally different from those on the rocky shore.

Spatial pattern plays a dominant role in regulating mussel larval settlement, postlarval recruitment, growth, and survivorship, as well as water flow, bedload transport, and species composition of infauna and epifauna within beds (Commito and Dankers, 2001; Commito et al., 2005; see Warwick et al., 1997 for a non-*Mytilus* example). Mussel beds generally have a hierarchical spatial structure (Fig. 1) consisting of irregularly shaped patches of all sizes, with large patches made up of smaller patches and so forth down to a spatial scale smaller than centimeters (soft-bottom examples: Snover and Commito, 1998; Kostylev and Erlandsson, 2001; Crawford et al., in press; rocky shore examples: Kostylev et al., 1997; Lawrie and McQuaid, 2001; Wootton, 2001; Guichard et al., 2003; Erlandsson and McQuaid, 2004).

How is this type of variability distributed across spatial scales? A number of spatial analysis techniques have been used in marine systems, such as fractal analysis (Snover and Commito, 1998; Kostylev and Erlandsson, 2001), spatial autocorrelation (Kostylev and Erlandsson, 2001), multiresolution sampling (Hewitt et al., 2002), geographic information systems applications (Remillard and Welch, 1992; Congleton et al., 1999; Zajac et al., 2003; Crawford et al., in press), principal coordinates of neighbor matrices (Borcard et al., 2004), and nested-ANOVA. Nested-ANOVA investigations have been used to estimate the proportion of total variance that occurs at each spatial scale. A review of that literature (with variance components calculated by us when not included in the article) demonstrates a wide variety of species patterns. The largest proportion of total variance can occur at the largest spatial scales studied (ephemeral green algae at locations 500–1000 m apart: Benedetti-Cecchi et al., 2001; barnacles at locations hundreds of kilometers apart: Jenkins et al., 2001); the smallest scales studied (infaunal bivalves in 10 cm diameter cores: Morrisey et al., 1992; ciliates in 1 ml surface samples: Santangelo et al., 2000; brown mussels in 10 × 10 cm quadrats: Lawrie and McQuaid, 2001; bryozoans on 10 × 10 cm collector panels: Benedetti-Cecchi et al., 2001); and intermediate spatial scales (infaunal polychates in 50 m diameter sites 100 m apart and amphipods in 2 m diameter plots 10 m apart: Morrisey et al., 1992; cockles *Cerastoderma edule* (L.) in sites hundreds of meters apart and *C. lamarcki* (Reeve) in bays thousands of meters apart: Lindegarth et al., 1995). Specifically for *M. edulis*, the greatest variability was observed at the smallest scale (0.1 $m^2$ sample units) in a soft-bottom system (Kostylev and Erlandsson, 2001) and at an intermediate scale (sites separated by at least 750 m within bays) on a rocky shore (Dudgeon and Petraitis, 2001). Investigations of this type have been conducted in different habitats, during different seasons, on different species, and on different measures of abundance within a species (e.g., density, biomass, recruitment). Thus, it is not surprising that no consistent pattern is evident.

The purpose of our study was to use a nested-ANOVA design to characterize the scales of mussel spatial variability in soft-bottom, intertidal *M. edulis* beds on the coast of Maine. Surprisingly, to our knowledge, this is the first time that soft-bottom mussel beds in North America have been analyzed in

Fig. 1. Mussel bed at Hammond Cove, Harrington, Maine, one of our study sites. For scale, height of undergraduate student in foreground = 162 cm.