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Hierarchical spatial structure in soft-bottom mussel beds

John A. Commito *, Wendy E. Dow [1], Benjamin M. Grupe [2]

Environmental Studies Department, Gettysburg College, Gettysburg, PA 17325, USA

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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.
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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

* Corresponding author. Tel.: +1 717 337 6030; fax: +1 717 337 8550.

E-mail address: jcommito@gettysburg.edu (J.A. Commito).

[1] Current address: Nicholas School of the Environment and Earth Sciences, Duke University Marine Laboratory, Beaufort, NC 28516, USA.

[2] Current address: Oregon Institute of Marine Biology, PO Box 5389, Charleston, OR 97420, USA.

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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), multi-resolution 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.

this way. Previous work in Maine has shown that soft-bottom mussel beds there have a fractal, hierarchical spatial distribution at all scales from that of an entire bed (Crawford et al., in press) down to millimeters (Snover and Commito, 1998). To the degree that mussel beds resemble pure, fractal, scale-invariant distributions, we expect that mussel variance is spread across all spatial scales. Numerous studies in the region have found large differences in mussel density and size–class structure among soft-bottom beds (compare values in: Commito, 1987; Commito and Boncavage, 1989; Snover and Commito, 1998; Commito and Rusignuolo, 2000; Commito et al., 2005) and in large patches at different positions within beds (Cusson and Bourget, 2005, and references therein). Therefore, we hypothesized that the largest proportion of the variance in mussel abundance occurs among beds and at coarse scales nested within beds.

2. Methods

2.1. Study site

The investigation was conducted at six intertidal, soft-bottom mussel beds (*M. edulis*) along 70 km (euclidean distance) of the coast in Hancock and Washington counties, eastern Maine, USA (Fig. 2). Air temperature extremes vary from winter lows of about −35 °C to summer highs of about 35 °C. Water temperature normally ranges from 0 to 15 °C, and salinity is usually about 30 PSU. The ecology of bare sediment and mussel bed habitats in this region has been well-studied (see Maine mussel bed references above; Commito, 1982a,b; Ambrose, 1984a,b; Commito and Shrader, 1985; Brown and Wilson, 1997; Congleton et al., 1999; Beal and Vencile, 2001; Beal et al., 2001; Commito and Rusignuolo, 2000; Commito and Tita, 2002). Mudflats and sandflats are usually dominated numerically by polychaetes, oligochaetes, amphipods, and nemerteans. The bivalves *Mya arenaria* L. and *Macoma balthica* L. and the polychaetes *Nereis virens* Sars, *Glycera dibranchiata* Ehlers, and *Nephtys incisa* Malmgren are the most important contributors to biomass, although often relatively uncommon numerically. In mussel beds, oligochaetes often assume greater importance than in bare sediment, and other infauna often have reduced abundances.

The six mussel beds were chosen from locations that are relatively accessible on foot from land. Both static (sediment characteristics) and dynamic (current

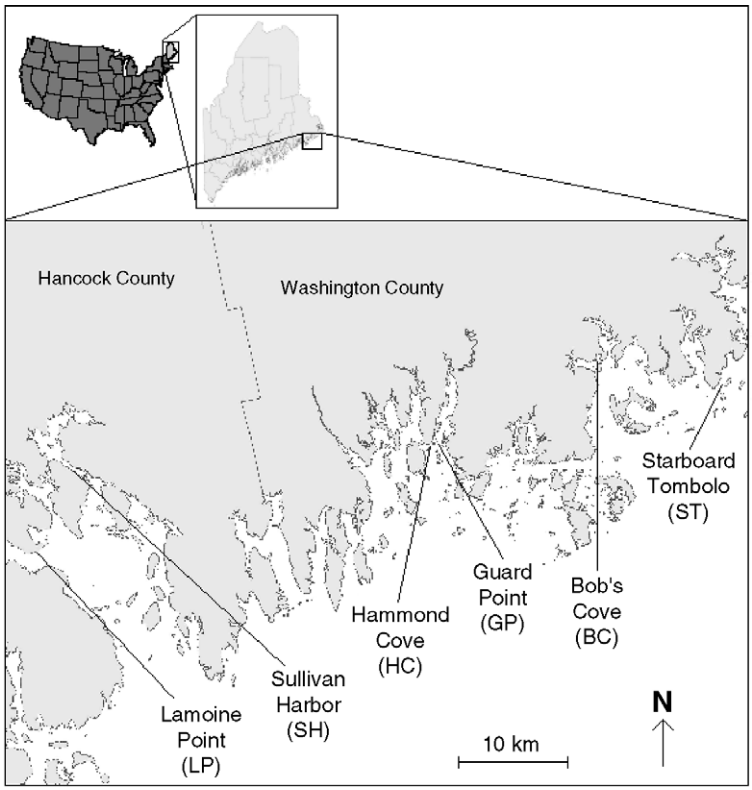

Fig. 2. Map of study area in eastern Maine, USA.

velocities and wave climate) environmental factors are important in regulating macrofauna abundances (Warwick and Uncles, 1980; Warwick et al., 1991). For mussels in particular, densities and spatial distributions are affected by water currents, exposure to storms, and winter ice that is moved by wind and water (McKindsey and Bourget, 2000; Commito and Dankers, 2001; Guichard et al., 2003; Cusson and Bourget, 2005). We ranked the bed locations according to Crawford's (2004) quantitative, GIS-based wind exposure index and a qualitative tidal flow index (Table 1). The proportion of fine sediment particles in the substrate tends to be inversely correlated with water velocity and degree of exposure to wind and storms (e.g., Ryan and Cooper, 1998). Fine particles are not attractive to settling mussel larvae. We measured the surface silt–clay fraction in our mussel beds because it provides information on both substrate suitability and the exposure and flow environments.

2.2. Field and laboratory procedures

We sampled a different mussel bed at low tide on each of six successive days, 10–15 August 2002. Mussel samples were taken with coring devices within a 120 m wide band running from the upper bed margin down the center of the bed to the low tide line. We used a nested sampling regime of six random Sites, i.e., beds were not chosen to be representative of particular conditions; any six beds would have sufficed; three Positions chosen at random points along a baseline down the center of the bed within each Site; two 6 m long Transects placed at random on a line parallel to the upper bed margin at each Position; two 1 m^2 Quadrats placed at random along each Transect; and two 20 cm tall × 16 cm diameter (cross-sectional area = 200 cm^2) Cores taken from randomly chosen corners within each Quadrat. The contents were sieved in situ on 0.5 mm mesh, and the residue was placed in buffered formalin, stained with Rose Bengal, and later sorted. The lengths of all live mussels and empty valves were measured to the nearest 0.1 mm. Adjacent to each of the mussel samples, we took a surface sediment sample with a 5.0 cm tall × 1.3 cm diameter (cross-sectional area = 1.33 cm^2) coring device. Sediment samples were wet sieved on a shaker through graded sieves and dried at 80 °C to constant weight. Mass was determined for each grain-size category, and we calculated the silt–clay fraction (i.e., the sediment that passed through a 0.062 mm mesh).

Table 1
Site characteristics for the six mussel beds in eastern Maine used in this study

Mussel bed	Location	GIS-based wind exposure index	Tidal flow index
Starboard Tombolo Open Tombolo, long fetch	Machiasport 44° 36′ 03″ N: 67° 23′ 36″ W	1	2
Guard Point Protected cove, long fetch	Harrington 44° 32′ 58″ N: 67° 46′ 04″ W	2	4
Hammond Cove Protected cove, long fetch	Harrington 44° 32′ 56″ N: 67° 46′ 20″ W	3	6
Lamoine Point Peninsula tip, short fetch	Lamoine 44° 27′ 17″ N: 68° 16″ 44″ W	4	3
Bob's Cove Protected cove, short fetch	Jonesboro 44° 37′ 23″ N: 67° 33′ 17″ W	5	5
Sullivan Harbor Narrow channel, short fetch	Franklin 44° 31′ 36″ N: 68° 14′ 10″ W	6	1

Rankings are from 1 (greatest exposure, fastest flow) to 6 (least exposure, slowest flow).

2.3. Statistical analysis

Data were analyzed with a pure random effects (Model II) nested-ANOVA (Sokal and Rohlf, 1995; Underwood, 1997) using the Statistix 8 analysis package (Analytical Software, 2003). The parameters tested were: surface sediment silt–clay fraction; total number of mussels; and numbers of recent recruits (<2 mm), all larger mussels (≥2 mm), and the subset of larger mussels that account for most of the percent cover (≥30 mm). $N = 144$ each for mussel samples and for sediment samples, where (6 Sites) × (3 Positions per Site) × (2 Transects per Position) × (2 Quadrats per Transect) × (2 Cores per Quadrat) = 144. Data were far from normally distributed, and variances were heteroscedastic, even when transformed. Although this situation violates the assumptions of ANOVA when testing hypotheses, it is not a problem for parameter estimation (Underwood, 1997). Our primary goal was to compute the proportion of total variance accounted for at each level in the nested design, so we proceeded with the analysis, as recommended by Benedetti-Cecchi (2001) and Bishop et al. (2002). In nested-ANOVA studies it is often the case that variability at a given spatial scale is less than predicted from the amount of variability found at a smaller scale, resulting in a negative estimate of variance (Fletcher and Underwood, 2002). Although researchers often deal with this problem by assigning a value of 0 to a negative variance, we

followed the "pool-the-minimum-violator" procedure recommended by Fletcher and Underwood (2002).

3. Results

3.1. Mussel bed characteristics

Overall, the mussel beds had a mean silt–clay fraction of 33.87%±2.56% (1 S.E.). Total mussel density was 23.52±7.47 individuals Core^{-1}, of which 10.42±6.00 individuals Core^{-1} were new recruits <2 mm long. Of the 13.13±2.54 individuals Core^{-1} that were ≥2 mm, about one-third (5.17±0.73 individuals Core^{-1}) were adults ≥30 mm.

However, these mean values mask large differences among Sites. The silt–clay fraction varied from 71.21%±0.03% (1 S.E.) at Bob's Cove down to 5.83%±0.01% at Lamoine Point (Fig. 3A). The sediment results were not in close agreement with the GIS-based wind exposure and qualitative tidal flow indices (Table 1). Moreover, the mussel parameters showed no consistent relationship with surface sediment or the exposure and flow rankings (Fig. 3B–E). Total mussel density (Fig. 3B) was quite variable from Site to Site, ranging from 1.33±

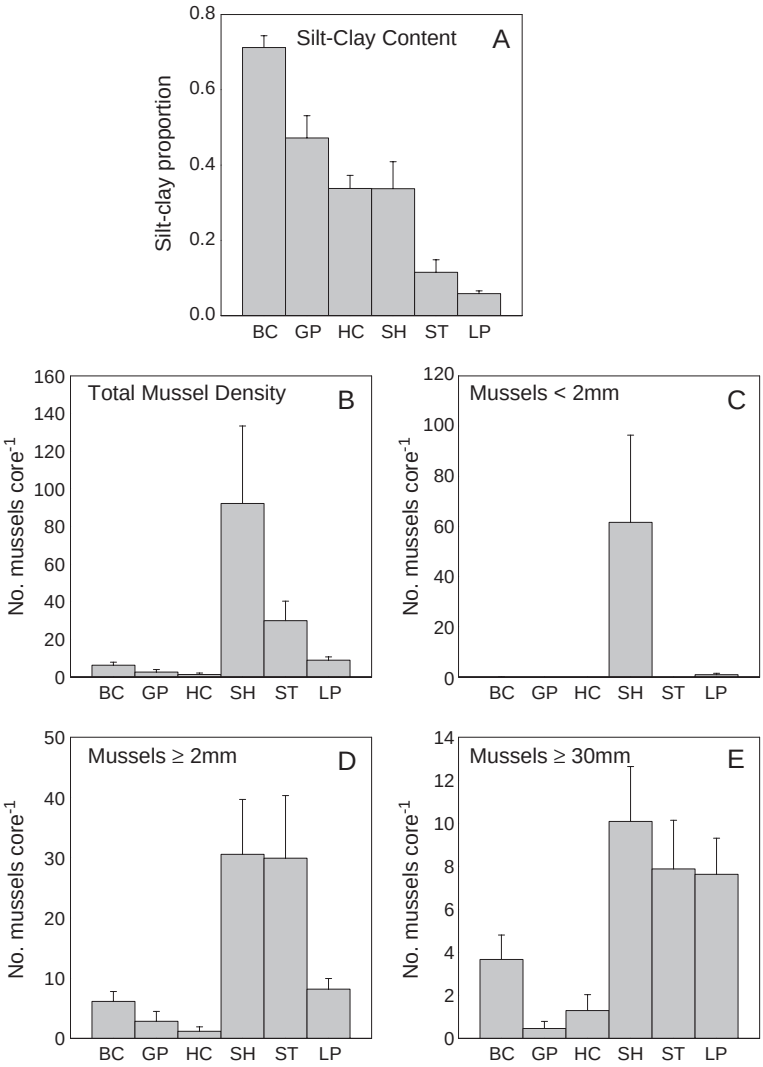

Fig. 3. Sediment and mussel parameters (mean±1 S.E.) for six mussel beds. In each panel, Sites arranged in the same sequence along the horizontal axis, from highest to lowest silt–clay fraction. BC = Bob's Cove, GP = Guard Point, HC = Hammond Cove, SH = Sullivan Harbor, ST = Starboard Tombolo, LP = Lamoine Point. A: Surface silt–clay content. B: Total mussel density. C: Density of mussels <2 mm. D: Density of mussels ≥2 mm. E: Density of mussels ≥30 mm. N=24 at each Site. Sediment core cross-sectional area=1.33 cm^2. Mussel core cross-sectional area=200 m^2.

0.75 individuals Core^{-1} at Hammond Cove to 92.17 ± 41.18 individuals Core^{-1} at Sullivan Harbor, yet these two Sites had the same silt–clay content (Fig. 3A). Site differences were even more pronounced for mussels <2 mm long, with Sullivan Harbor accounting for virtually all the new recruits (Fig. 3C). Larger mussels were somewhat more equitably distributed across Sites, but substantial differences still existed (Fig. 3D–E). Despite the high level of variability, there was a trend of higher mussel densities, especially for large mussels, at Sites with low silt–clay content and high exposure or flow rankings.

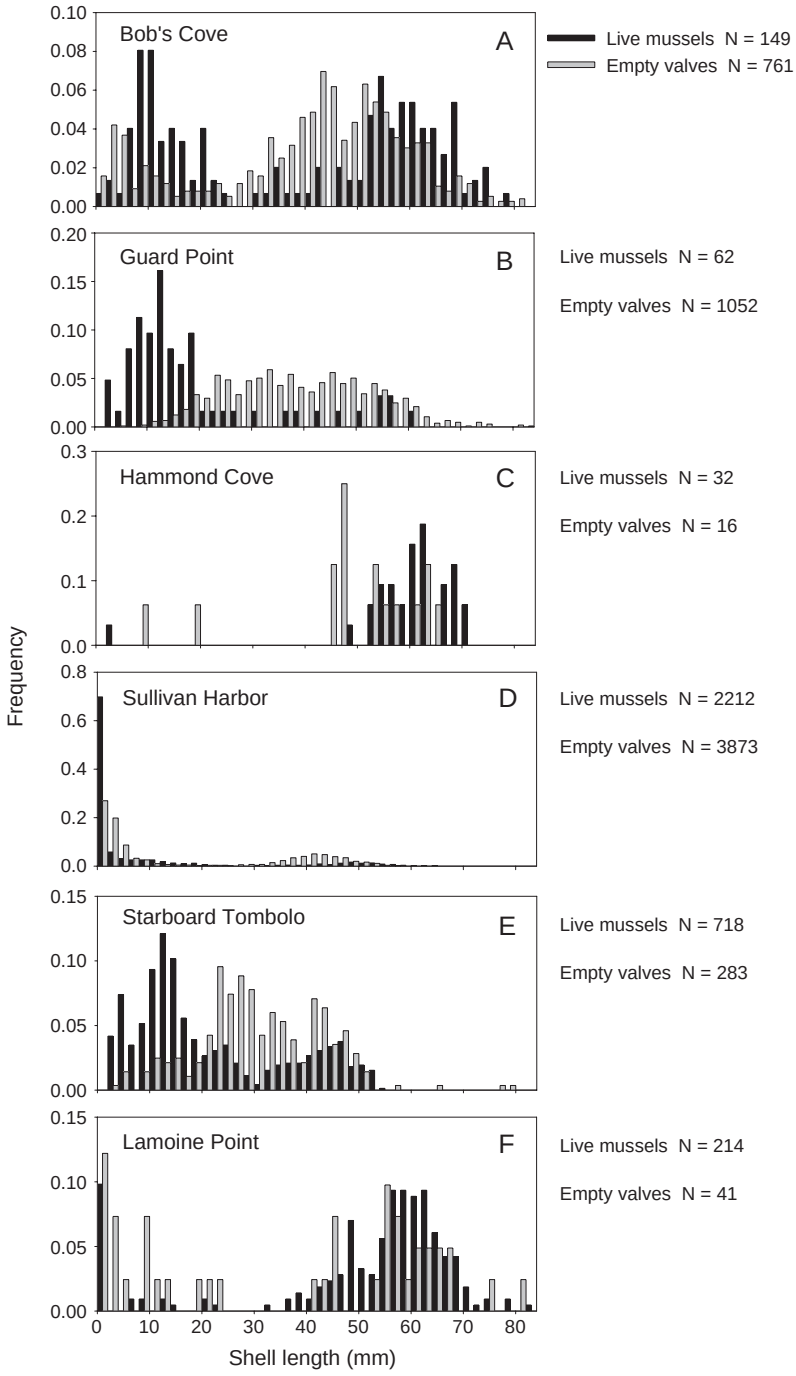

Fig. 4. Size–class histograms of live mussels and empty valves for six mussel beds. *N* values are from 24 mussel cores with cross-sectional area = 200 cm^2.

The size–class histograms for live mussels and empty valves provide additional details about the differences in population structure across Sites (Fig. 4). Large Site-to-Site differences in size–class structure are clearly evident. However, all six Sites show at least some size–class bimodality in the living population, often with death assemblage valves having higher proportional abundances than the live mussels in the middle size classes. The results suggest similar population dynamics across Sites.

3.2. Hierarchical mussel bed structure

Nested-ANOVA results for the surface silt–clay fraction demonstrated that the largest proportion of total variance (nearly half), was at the Site level, the largest spatial scale in our investigation (Table 2). The smallest variance components for the silt–clay fraction were at the smallest spatial scales, with intermediate variance at intermediate spatial scales. The nested-ANOVA results indicated significant differences in the silt–clay fraction at every level.

None of the mussel parameters followed the pattern observed for the sediment (Table 2). The Site level never accounted for a large proportion of total variance, regardless of the mussel parameter considered. Sites accounted for <4% of the total variance in total mussel density (Table 2). The largest variance component for total mussel density (nearly half of the total) was at the Quadrat level, followed by one-third of the total at the Core level. Virtually the same pattern was observed for mussels <2 mm long (Table 2) because new recruits accounted for such a large percentage of the total mussel density. For larger mussels, both ≥2 mm and ≥30 mm, the largest variance component was at the next higher level in the hierarchy, the Transect level (Table 2).

4. Discussion

4.1. Where is the variance?

Based on the literature and our own field observations in eastern Maine, we hypothesized that Sites and Positions accounted for most of the spatial variance in soft-bottom mussel beds. We rejected both hypotheses. Sites and Positions were not important in explaining variation in total mussel density, density of new recruits, or density of larger mussels. Most variation occurred at smaller spatial scales, specifically at the 1 m^2 Quadrat scale for new recruits and total mussels and at the 6 m long Transect scale for larger mussels.

Several patterns emerged from the analysis (Table 3). First, most of the variance in total mussel density and other mussel parameters was at smaller scales than, and not closely linked to, variance in the silt–clay fraction of surface sediment. Second, variance in total mussel density was due primarily to variance in recruitment. Third, variance in new recruits occurred at smaller spatial scales than variance in larger, older mussels. Fourth, for every mussel parameter, the level with the greatest variance was always lower in the spatial hierarchy than the level with the smallest variance.

Kostylev and Erlandsson (2001) performed a detailed spatial analysis of shallow subtidal soft-bottom mussel beds in Sweden. Using variograms, spatial autocorrelation, and nested-ANOVA on mussel biomass, they observed significant variation across spatial scales. In order to make our analysis and theirs more compatible, we used their ANOVA tables to compute the variance components for the three locations they studied. They did not compare locations (comparable to our Sites). They sampled within locations using 0.1 m^2 sampling units at 64, 32, 16, 8, and 4 m scales. At one location (fast water currents and sand–gravel sediment), the

Table 2
Variance components (V. c.) and percent variance components (% v. c.) for six mussel beds

Source	Mussel bed parameter									
	Silt–clay fraction		Total mussels		Mussels <2 mm		Mussels ≥2 mm		Mussels ≥30 mm	
	V. c.	% v. c.	V. c.	% v. c.	V. c.	% v. c.	V. c.	% v. c.	V. c.	% v. c.
Sites	**0.0457**	**44.36**	310.8	3.80	166.6	3.17	48.43	5.10	7.597	9.57
Positions	0.0210	20.33	1544.4	18.87	462.0	8.79	101.72	10.70	0.105	0.13
Transects	0.0224	21.73	–[a]	–[a]	4.8	0.09	**455.96**	**47.98**	**45.684**	**57.55**
Quadrats	0.0033	3.15	**3603.0**	**44.03**	**2768.7**	**52.69**	213.23	22.44	4.639	5.84
Cores	0.0108	10.43	2725.7	33.31	1852.8	35.26	131.03	3.79	21.361	26.91
Total	0.1031	100	9023.3	100	5254.8	100	950.37	100	79.386	100

N=144. Silt–clay core cross-sectional area=1.33 cm^2. Mussel core cross-sectional area=200 cm^2.
Largest variance component in bold.
[a] "Pool-the-minimum-violator" applied (Fletcher and Underwood, 2002).

Table 3
Summary of sediment and mussel variance components for six mussel beds

Parameter	Lowest variance	Highest variance
Silt–clay fraction	Quadrats	Sites
Total mussels	Transects	Quadrats
Mussels < 2 mm	Transects	Quadrats
Mussels ≥ 2 mm	Sites	Transects
Mussels ≥ 30 mm	Positions	Transects

N = 144. Silt–clay core cross-sectional area = 1.33 cm^2.
Mussel core cross-sectional area = 200 cm^2.

largest variance component was at the 32 m scale, and the second largest was at the smallest scale (their 0.1 m^2 sampling units). At the other two locations (fast water currents and sand–gravel sediment; slow water currents and mud sediment), the largest variance components occurred at the smallest spatial scale. Overall, it was the smallest spatial scale that explained most of the variation in the spatial distribution of mussel biomass at their three locations.

Our beds in Maine were intertidal rather than subtidal, and we examined mussel densities rather than biomass, so direct comparisons with the Kostylev and Erlandsson (2001) study cannot be made. But to the extent that our systems were ecologically similar and that density and biomass are correlated (especially for large mussels), both their investigation and ours indicate that events occurring at small to intermediate spatial scales are important in structuring soft-bottom mussel beds. Lawrie and McQuaid (2001) and Erlandsson and McQuaid (2004) reached a similar conclusion for the mussel *Perna perna* (L.) on hard bottoms in South Africa. Likewise, the largest variance for a variety of intertidal organisms in other systems occurred at small spatial scales, not the large scales we had initially assumed for Maine soft-bottom mussel beds (Morrisey et al., 1992; Santangelo et al., 2000; Benedetti-Cecchi et al., 2001).

4.2. Mechanisms controlling spatial pattern

Previous work in soft-bottom systems has demonstrated the importance of both static (sediment characteristics) and dynamic (current velocities and wave climate) environmental factors in regulating macrofauna abundances (Warwick and Uncles, 1980; Warwick et al., 1991). Surprisingly, the mussel parameters at our six beds showed no consistent relationship with surface sediment or the exposure and flow rankings. This result suggests that the mussel beds reported on here are responding to different or additional factors. Much is known about the factors that control spatial patterns in rocky shore mussel beds, including locations in Maine and eastern Canada (e.g., Archambault and Bourget, 1996; Leonard et al., 1998, 1999; Petraitis and Latham, 1999; Dudgeon and Petraitis, 2001; Hunt and Scheibling, 2001; Petraitis et al., 2003; Bertness et al., 2004a). Yet control mechanisms in soft-bottom systems in Maine and elsewhere remain poorly understood (Nehls and Thiel, 1993; Reusch and Chapman, 1997; Commito and Dankers, 2001; Dankers et al., 2001; Cusson and Bourget, 2005; van de Koppel et al., 2005).

Work done on the Maine rocky shore may provide some insight into the mechanisms that control mussel abundance and spatial pattern at the soft-bottom sites in our study. Mussels tend to dominate the rocky shore in locations with rapid water flow, while fucoid algae dominate where flow is slow (Bertness et al., 2004b). Where mussels are found, their abundance is positively correlated with water flow due to higher recruitment and lower predation rates (Bertness et al., 2004b). Scale-dependent processes of ice scour and predation can create and maintain areas of mussels or fucoid algae, with mussel abundance being positively correlated with the size of clearings due to higher recruitment and lower predation rates (Petraitis and Dudgeon, 2004).

Consistent with Bertness et al. (2004b), our mussel size–class distributions were somewhat bimodal, possibly resulting from high rates of predation on mid-sized mussels predicted in beds with the generally slow flow associated with soft-bottoms, and the Sullivan Harbor bed had the fastest water flow and greatest density of all sizes of mussels, including new recruits. Consistent with Petraitis and Dudgeon (2004), at our soft-bottom mussel beds the spatial structure was extremely patchy, mussel parameters were highly variable from Site to Site, and neither total density nor recruitment appeared to be closely linked to exposure and flow rankings.

It is therefore possible that the spatial structure observed at our mussel beds results from ecological processes occurring at several spatial scales. Mussel recruitment may be controlled by small-scale variations in bottom topography (including the presence of mussels themselves) and turbulent flow over the bottom (Svane and Ompi, 1993; Butman et al., 1994; Commito and Rusignuolo, 2000). As the recruits get older, the average flow rate operating over larger spatial scales assumes greater importance as it delivers food particles and regulates predation (Bertness et al., 2004b). Storm events and ice scour can also operate on relatively large scales and may create spatial heterogeneity at those scales by removing adult mussels in the winter (Nehls and Thiel, 1993; Reusch and Chapman, 1997; McKindsey

and Bourget, 2000; Petraitis and Dudgeon, 2004; Cusson and Bourget, 2005). This set of scale-dependent processes might explain the results obtained at the mussel beds in our study: the greatest spatial variation for the small, young mussels was at the Quadrat level, shifting up to the Transect scale for the large, old mussels.

However, as reasonable as this model might appear, Occam's Razor asks for the most simple explanation first. Research currently underway in our laboratory demonstrates that it might not be necessary to invoke a suite of ecological processes operating at different spatial scales to produce the complex spatial structure observed in soft-bottom mussel beds. Our simple cellular automaton mussel bed model acknowledges the fact that soft-bottom mussel beds are different from rocky shore beds. On soft-bottoms, mussel larvae are more constrained. They very rarely settle onto bare sediment substrate, they seem to prefer existing mussels and empty shells to other roughness elements like gravel, and patches may not grow outwards as easily over soft sediment (Dankers et al., 2001). Our model has only two rules: “mussel beds grow” and “they grow from larvae landing on existing mussel patch edges.” This model produces complex, patchy, hierarchically structured, fractal mussel beds with qualitative and quantitative characteristics similar to actual soft-bottom beds. An important feature of this model result is that patchiness occurs even without the removal processes of storms, ice scour, and predation.

Thus, soft-bottom spatial structure may be controlled in ways that are fundamentally different from those on rocky shores. Soft-bottom mussel beds may be a good example of a self-organizing system. Self-organized systems are characterized by complex, hierarchical, power–law structure, which is observed in soft-bottom beds in Maine and elsewhere (Snover and Commito, 1998; Commito and Rusignuolo, 2000; Kostylev and Erlandsson, 2001; Crawford et al., in press). Of course, natural and model beds represent imperfect, statistical fractals, not precise, mathematically pure fractals. Thus, they are not perfectly scale-free, which may explain why we did not observe the same amount of variance at each level in our nested design.

We are not saying that removal processes are unimportant in soft-bottom beds. Rather, we surmise that mussel removal events may be superimposed over an already complex spatial structure resulting from self-organized recruitment patterns particular to soft-bottom beds. If self-organization of beds is important, then commercial mussel fisheries may present particularly intractable management problems because dredging removes live and dead mussels that serve as settling substrate for new recruits (Herlyn and Millat, 2000; Dolmer, 2002; Dolmer and Frandsen, 2002; Riis and Dolmer, 2003).

5. Conclusions

Our results indicated that Site differences in mussel abundance in intertidal, soft-bottom beds were not tightly linked to the surface sediment silt–clay fraction or to wind exposure and tidal flow rankings. Moreover, we failed to support our hypothesis that the largest amount of total mussel variance occurs at the Site and Position scales. These scales were among the least important in explaining mussel variance.

We found that most of the mussel variance occurred at relatively small spatial scales (1 m^2 Quadrats and 6 m long Transects). However, no single scale explained more than about half the mussel variance, and no single scale was best at explaining all the mussel parameters. The factors responsible for creating and maintaining hierarchical spatial structure are poorly understood for intertidal, soft-bottom mussel beds. 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.

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