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The role of colonization in establishing patterns of community composition and diversity in shallow-water sedimentary communities

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ABSTRACT

To determine whether pattern and diversity in benthic sedimentary communities are set primarily at colonization or by post-settlement biological interactions, we collected faunal cores and conducted reciprocal sediment transplant experiments at a sandy and a muddy site at 12 m depth, ~3 km apart off New Jersey. Multivariate analyses of cores collected at these sites in September 1994 indicated differences in the taxa determining local pattern, with the bivalve *Spisula solidissima* and the polychaete *Polygordius* sp. being dominant at the sandy site, and oligochaetes, several polychaete species, and the bivalve *Nucula annulata* dominant at the muddy site. Individual cores from the sandy site were significantly less diverse than those at the muddy site. Short-term experiments (3–5 d) were deployed by divers at three different times (August-September, 1994). Replicate trays (100 cm^2) filled with azoic sand or mud were placed flush with the ambient seafloor at both sites. Multivariate comparisons indicated that sediment treatment in trays played a greater role in determining colonization patterns in the first experiment, site played a greater role in the second, and both variables contributed in the third. This pattern suggests that larval settlement and habitat choice played an important role in the first and third experiments, and that local transport of recently settled juveniles from the surrounding sediments was important in the second and third experiments. Sandy-site trays had significantly lower diversity than muddy-site trays, but there was no effect of sediment type in trays on diversity of colonizers. These experiments focused on small spatial scales and three short time periods, but they demonstrate that species patterns in some environments may be set by habitat selection by larvae and by juvenile colonization from the surrounding community. Post-colonization processes such as predation and competition likely play a major role for some species, but patterns of initial colonization corresponded well with those in the local community.

1. Introduction

Recent interest in biodiversity of marine systems has punctuated how little we know about why pattern and diversity vary spatially in the oceans and how they are maintained (e.g. National Research Council, 1995; Snelgrove, 1999), although there have been

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significant recent advances in understanding the importance of biodiversity (Stachowicz *et al.,* 1999; Emmerson *et al.,* 2001). The processes influencing patterns of community composition and diversity in marine habitats include those that operate pre- and post-colonization. Post-colonization processes include abiotic disturbance (Sanders, 1969), predation (Peterson, 1979) and competition (Wilson, 1991). Differences in larval (Roughgarden *et al.,* 1988; McConnaughey *et al.,* 1992; Clancy and Cobb, 1997) and juvenile supply (e.g. Emerson and Grant, 1991; Whitlatch *et al.,* 1998) as well as larval (Butman, 1987) and juvenile (Olivier *et al.,* 1996) habitat selection are colonization-related processes that could influence benthic pattern. Although the relative importance of recruitment limitation in sedimentary systems remains contentious (Ólafsson *et al.,* 1994; Snelgrove and Butman, 1994; Woodin, 1999), there is acceptance that larval supply plays a significant role for some benthic species at multiple temporal (Wing *et al.,* 1995) and spatial (Cameron and Rumrill, 1982; Butman, 1987) scales.

If community structure is set at colonization, it would be reasonable to expect that patterns of initial colonization, either through settling larvae or immigrating juveniles, should be similar to patterns in local communities. If post-colonization processes play a greater role in determining pattern, then a link between initial colonization patterns and the local community would be less likely. A similar argument has been made for hard substrate communities (Smith and Witman, 1999). These predictions are complicated by the fact that pattern and diversity in colonizers and local communities may be both time- and space-dependent; dissimilarity in pattern may simply mean that the timing or spatial scale of sampling was inappropriate. If similar patterns in ambient communities and initial colonizers were observed, however, this would suggest that relative species abundances at colonization may set pattern in local communities.

Laboratory still-water (e.g. Mortensen, 1921), flume flow (e.g. Butman *et al.,* 1998; Snelgrove *et al.,* 1998), and field experiments (Snelgrove *et al.,* 1999) have demonstrated that larvae of some species of marine invertebrates can select for sediments which are characteristic of their adult environment. Differences in larval settlement in geographically proximate sedimentary habitats suggest that habitat selection (Günther, 1991) or variability in the supply of colonizers (Eckman, 1979; Cameron and Rumrill, 1982) are important in setting spatial pattern for some taxa. Other studies have found no differences in initial settlement in different sediment types (e.g. Smidt, 1951; Muus, 1973), suggesting that post-settlement processes are more important. Most studies of larval and early post-settlement habitat selection have focused on patterns of individual species and often at scales of centimeters (e.g. Eckman, 1979; Butman *et al.,* 1988), but sediment choice experiments in contrasting sedimentary environments could link initial colonization and local community patterns. Although a number of field studies have examined the response of infauna to experimental sediments (e.g. McCall, 1977; Zajac and Whitlatch, 1982; Thrush *et al.,* 1991), most have examined time scales that reflect recruitment (weeks to months) rather than initial colonization (hours to days) and, therefore, may incorporate competition and predation (but see VanBlaricom, 1982; Savidge and Taghon, 1987). Moreover, few *in situ* sediment choice (habitat selection) experiments have been conducted to date. The experiments reported here focus on habitat selection during initial colonization.

To contrast the roles of colonizer supply, active habitat selection, and post-colonization processes in determining community structure, we compared local faunal composition in two sedimentary environments and conducted short-term sediment transplant experiments to evaluate how patterns of initial colonizers compared to those in the local community. We have reported previously on settlement of individual taxa in these experiments (Snelgrove *et al.,* 1999), and here expand on that work to contrast patterns of community composition and diversity. Here we look at colonization during three time periods when larval settlement and early post-settlement redistribution could occur, and focus on small-scale (100 cm^2) composition patterns at two shallow continental shelf sites separated by several kilometers. The macrofaunal communities at these sites represent a regional species pool defined as the ridge and swale communities of the Mid-Atlantic Bight continental shelf (Boesch, 1979), inshore of the permanent cold pool.

2. Materials and methods

a. Study area

Faunal cores and experimental sedimentary tray data were collected from two sites at the LEO-15 study area (Von Alt and Grassle, 1992) on Beach Haven Ridge, a shore-oblique ridge ~3 km off the coast of New Jersey that is ~15 m deep, 5 km long and 1.5 km wide. A sandy site (ø ~ 1.0, Craghan, 1995) on the southern landward side of the ridge (39° 27.69′ N, 74° 15.81′ W) and a contrasting muddy-sand site, hereafter the "muddy site" (ø ~ 3.7, Craghan, 1995), on the northern, landward side (39° 29.29′ N, 74° 14.48′ W) were chosen for the study.

b. Faunal cores and sediment trays

Faunal composition at the sites was determined by random coring (diameter 7 cm) to ~10 cm into the sediment in September 1994 (see randomization scheme of Morrisey *et al.,* 1992). Nine replicate cores were collected at the muddy site, and nine pairs of crest and trough samples were collected at the rippled sandy site. Samples were processed over a 300-μm sieve, fixed in 10% formalin, and promptly transferred to ethanol with Rose Bengal.

Surface sand or mud was collected in bulk from each site during the summer of 1994, frozen, rinsed with freshwater, pushed through a 1 mm sieve to remove shell fragments and large, dead invertebrates, and refrozen until needed. Sediment trays (sediment surface area 100 cm^2, depth 2 cm, described by Snelgrove, 1994) were filled with thawed sediments, and then sealed with lids during transport to and from the bottom. At both sites, three replicates each of sand and mud treatments (where treatment refers to type of sediment and thus, collection location) were deployed flush with the ambient seafloor by divers. At the sandy site, trays were placed so that the lip was between crests and flush with the surrounding sediment. Treatments were haphazardly interspersed, separated by several meters and oriented along a depth contour perpendicular to the predominant tidal flow. Lids were removed, and trays were left *in situ* for three 3–5 day experiments (depending on date) in August and September 1994. Retrieved trays were immediately processed over a 100-μm sieve and preserved as described above. During the 4 Aug experiment, only one of the sand treatment trays was recovered at the muddy site.

The use of different sieve sizes for the local community cores and the tray settlers was deliberate, in that the cores were used to evaluate adult assemblages whereas the trays were deployed to evaluate initial colonizers. Nonetheless, this difference in methodology necessitated separate analyses for cores and trays. In most instances, core fauna could be identified to species; however, many of the individuals in trays were very recent settlers and taxonomic resolution below the family level was often not possible. Initial analyses of cores on the full community data sets for the two sites were repeated with the collapsed species groupings used for trays. The patterns were very similar, and results from the collapsed data are reported.

c. *Data analysis*

Community composition was compared between the two sites using the CNESS (chord-normalized expected species shared) approach (Trueblood *et al.,* 1994). CNESS is based on the number of expected species shared in a random draw of *n* individuals (set here at 10) from two samples. Samples were then clustered using unweighted, pair-group mean average sorting of CNESS dissimilarities. A metric scaling of CNESS was analyzed by principle components analysis of hypergeometric probabilities (see Trueblood *et al.,* 1994). The first two sets of component scores provide a two-dimensional metric scaling of CNESS, and because the scaling is metric, it is possible to overlay a Gabriel Euclidean distance biplot (Gabriel, 1971), where the length and direction of species vectors are proportional to the CNESS variation attributable to that species. For clarity, only species that contributed >5% to CNESS variation were retained from the analysis for inclusion in biplots. To provide a more objective interpretation of between-site taxonomic differences, a discriminant function analysis was also run with site as the factor. Although discriminant function analysis allows hypothesis testing, the assumption of multivariate normality is inappropriate for these species data, and we present it as a way of evaluating which taxa are responsible for the between-site differences observed in the PCAH plots. Thus, we arbitrarily define those taxa with p-values < 0.05 as most important without attaching statistical significance to the cutoff value. These results are difficult to compare directly with those produced by ANOVA because treatment, site, and treatment x site effects are not partitioned in the discriminant function analysis.

Diversity of local community cores was compared between sites by plotting Hurlbert rarefaction curves (Hurlbert, 1971) for individual cores. One-way ANOVA comparisons of Shannon-Weiner diversity (H'), evenness (J'), Hurlbert's $E(S_n)$ with $n = 100$ individuals, and species richness (number of species per core) were made with site as the factor.

Community data in trays were analyzed using the multivariate approaches described above. Discriminant function analysis was also run for each of the three experiments for the reasons outlined above, but in this case the choice of function was treatment, site, or both, depending on which variables the PCAH plots indicated were important in describing data patterns. Diversity was compared between sites and treatments by plotting Hurlbert rarefaction curves. Statistical comparison was made by ANOVA of $E(S_n)$ with $n = 100$ individuals, Shannon-Weiner diversity (H'), evenness (J), or species richness. The model for these comparisons was $y = \mu + \text{date} + \text{site} + \text{treatment}$, where y refers to the measure H', J, or $E(S_{100})$ accordingly, μ is a mean constant, date is date of experiment, site refers to sand or mud site, and treatment refers to sandy or muddy treatment. Site and treatment were treated as fixed variables and date was treated as random. An initial run of a full model indicated no significant interaction terms, and the model was therefore run with only main effects. Homogeneity of variance tests indicated that no data transformation was needed. Richness (number of taxa per tray) was compared for $\log(x + 1)$ transformed data.

3. Results

a. *Local community composition and diversity*

The local community at the sandy site was dominated by the surfclam *Spisula solidissima* and the annelid worms *Polygordius* sp. and *Tharyx* spp. (*Tharyx kirkegaardi* and *T. acutus* were both present but were pooled for comparison with tray experiments, where individuals could only be identified to genus.) These polychaetes also occurred at high densities at the muddy site, where the bivalves *Nucula annulata* and *Tellina* spp., oligochaetes (mostly *Tubificoides* spp.), and *Mediomastus ambiseta* were also abundant (Fig. 1). Of these taxa, *S. solidissima* was significantly more abundant at the sandy site and oligochaetes and *M. ambiseta* were significantly more abundant at the muddy site.

Cluster analysis and PCAH analysis of faunal cores indicate that the fauna at the sandy and muddy sites is generally different (Fig. 2); whether cores from the sandy site were collected from crests or troughs appeared to have no bearing. Gabriel biplots suggest that *N. annulata, M. ambiseta,* oligochaetes, and to a lesser extent *Tharyx* spp. were important taxa in the muddy site community, whereas *S. solidissima* and *Polygordius* sp. were important descriptors of the sandy site. The second axis, which explains much less variation in the data than axis 1, may represent within-site patchiness. These taxa were all important in the discriminant function analysis, but several other taxa at the muddy site discriminated cores from those at the sandy site (Table 1).

Individual cores at the sandy site were generally less diverse than those at the muddy site (Fig. 3). Although there is some overlap in curves, this general conclusion is supported by significant between-site differences in the ANOVA comparisons of Shannon-Weiner ($\bar{x}_{\text{muddy site}} = 1.7, se = 0.1, \bar{x}_{\text{sandy site}} = 1.1, se = 0.1, F = 233.1, P = 0.000$) and $E(S_{100})$ ($F = 320.2$, $P = 0.000$) diversity (Fig. 3). ANOVA of species richness indicated that significantly more species occurred in cores from the muddy site than at the sandy site (muddy

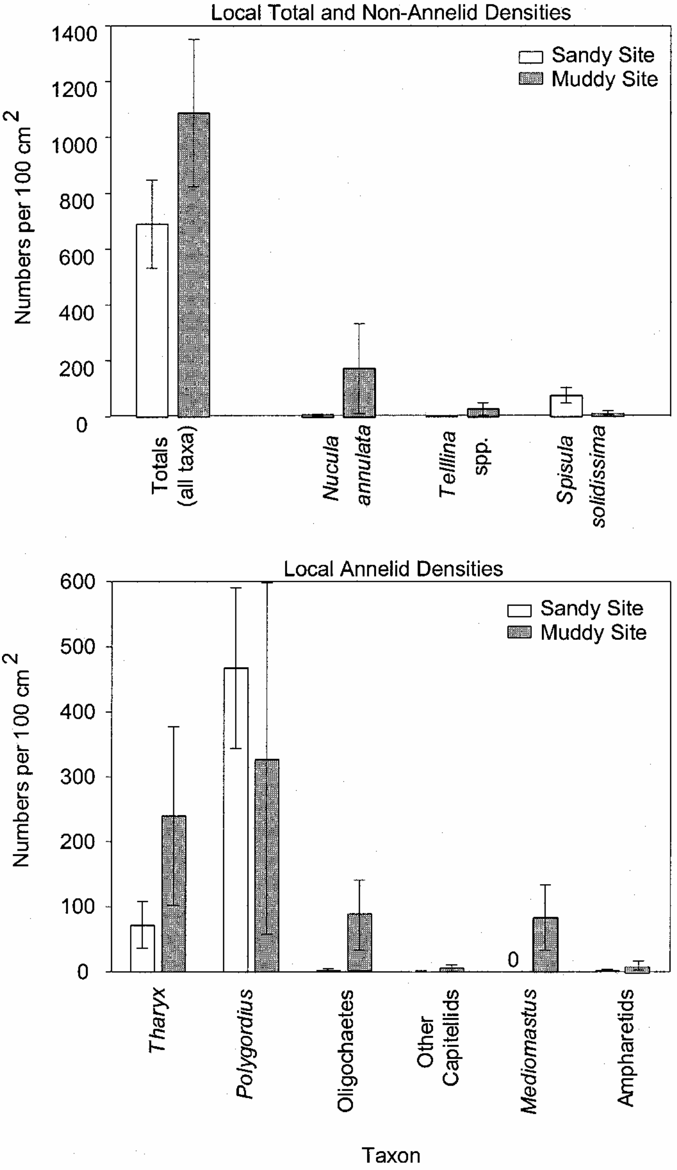

Figure 1. Means and 95% confidence intervals for non-annelid and annelid macrofauna in community cores from sandy and muddy sites in September 1994. Taxa shown are those that the PCAH analysis indicated were most important in describing community structure in ambient cores and sediment trays. Abundance converted from mean number of individuals core^{-1} (area 38 cm^2) to mean number 100 cm^{-2}. Totals in upper panel refer to all taxa including annelids.

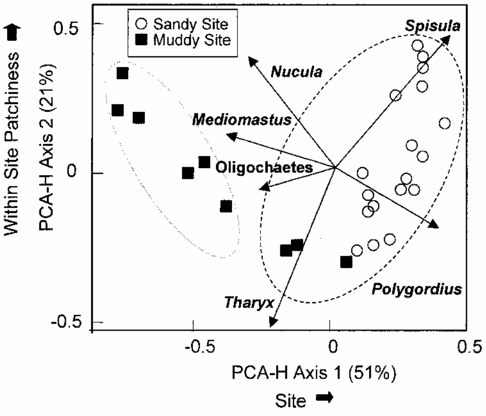

Figure 2. Cluster analysis of local community cores from sandy ($n = 18$) and muddy ($n = 9$) sites based on CNESS dissimilarity with $m = 10$ individuals. Percentages on axes denote variation explained by each of the principal components, and secondary axis labels denote interpretations of the principal components. PCAH ordination species vectors overlaid on community ordination describe which species drive spatial pattern. Dashed ovals indicate major clusters.

site $\bar{x} = 16.9$ species, $se = 1.0$, sandy site $\bar{x} = 11.5$ species, $se = 0.7$, $F = 272.0$, $P = 0.000$). Evenness was significantly higher at the muddy site ($\bar{x}_{\text{muddy site}} = 0.60$, $se = 0.04$, $\bar{x}_{\text{sandy site}} = 0.45$, $se = 0.02$, $F = 310.7$, $P = 0.000$).

b. *Tray faunal composition and diversity*

Many of the abundant taxa in the communities at the two sites were also abundant in tray treatments (Fig. 4). Significant site and treatment effects are difficult to discern because

Table 1. Taxa important in differentiating between Treatment or Site effects in three field experiments (identified by date) as determined by Discriminant Function Analysis. Taxa important in differentiating muddy site or mud treatment effects are shown in bold, and those not in bold were important to sandy site or sand treatments. "Other capitellids" refers to capitellid taxa other than *M. ambiseta.*

Local community (site)	Aug. 1–4 treatment	Aug. 16–19 site	Sept. 14–19 treatment	Sept. 14–19 site
Ampharetids		**Ampharetids**	**Ampharetids**	
		Other capitellids	**Other capitellids**	
Notomastus luridus				
		Parougia caeca		
***Glycera* spp.**				
Mediomastus ambiseta		***M. ambiseta***		***M. ambiseta***
Oligochaetes	**Oligochaetes**	**Oligochaetes**		**Oligochaetes**
Onuphis eremita oculata				
Aricidea catherinae		***A. catherinae***		***A. catherinae***
		Phyllodocids		
Spionids				
***Tharyx* spp.**		***Tharyx* spp.**		***Tharyx* spp.**
Nucula annulata	***N. annulata***	***N. annulata***		
***Tellina* spp.**		***Tellina* spp.**		
Spisula solidissima	*S. solidissima*	*S. solidissima*		
Edotea triloba				
Unciola sp.				
	Gastropods			

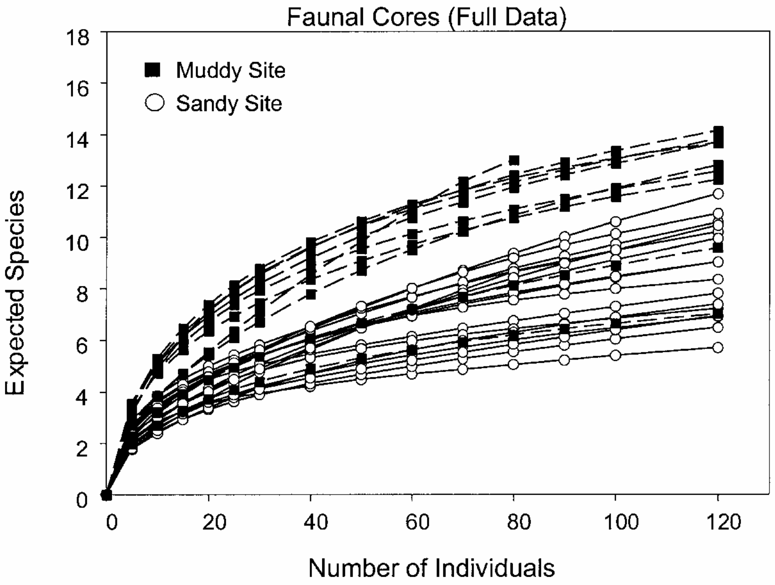

Figure 3. Hurlbert rarefaction of local community faunal cores at the sandy and muddy sites.

dates were pooled to simplify presentation, and colonization differed significantly for many taxa among dates. Nonetheless, significantly more *S. solidissima* and *Polygordius* sp. colonized sand than mud treatments, whereas significantly more capitellids (*Capitella* spp. or *Capitomastus* spp.), oligochaetes, and ampharetids colonized mud treatments (see Snelgrove *et al.*, 1999). A number of between-site differences were also observed. None of the abundant species were significantly more abundant at the sandy site, but significantly more *N. annulata, Tellina* spp., capitellids, and oligochaetes colonized trays at the muddy site. Between-site differences were not significant for other taxa, although significant interaction terms related to site were observed for *S. solidissima* and *Tharyx* spp., indicating that differences between sites occurred in individual experiments but were not consistent among experiments.

The PCAH and cluster analyses for the 1–4 Aug. experiment indicated separate groupings for the mud and sand treatments (Fig. 5-top panel); the first axis of the PCAH plot, which explained the majority of the data variation, clearly separated treatments rather than sites. *S. solidissima* contributed strongly to sand treatments, and oligochaetes and *N. annulata* contributed strongly to mud treatments. These same taxa were important in the discriminant function analysis based on treatment, but gastropods were also important in sand treatments (Table 1).

For the 16–19 Aug. experiment, samples did not group clearly by either sediment treatment or deployment site, but sites were discretely segregated on the PCAH plot along a 45° axis (Fig. 5-middle panel). This pattern suggests that site was more important than treatment in this experiment. Ampharetid and capitellid polychaetes were important in

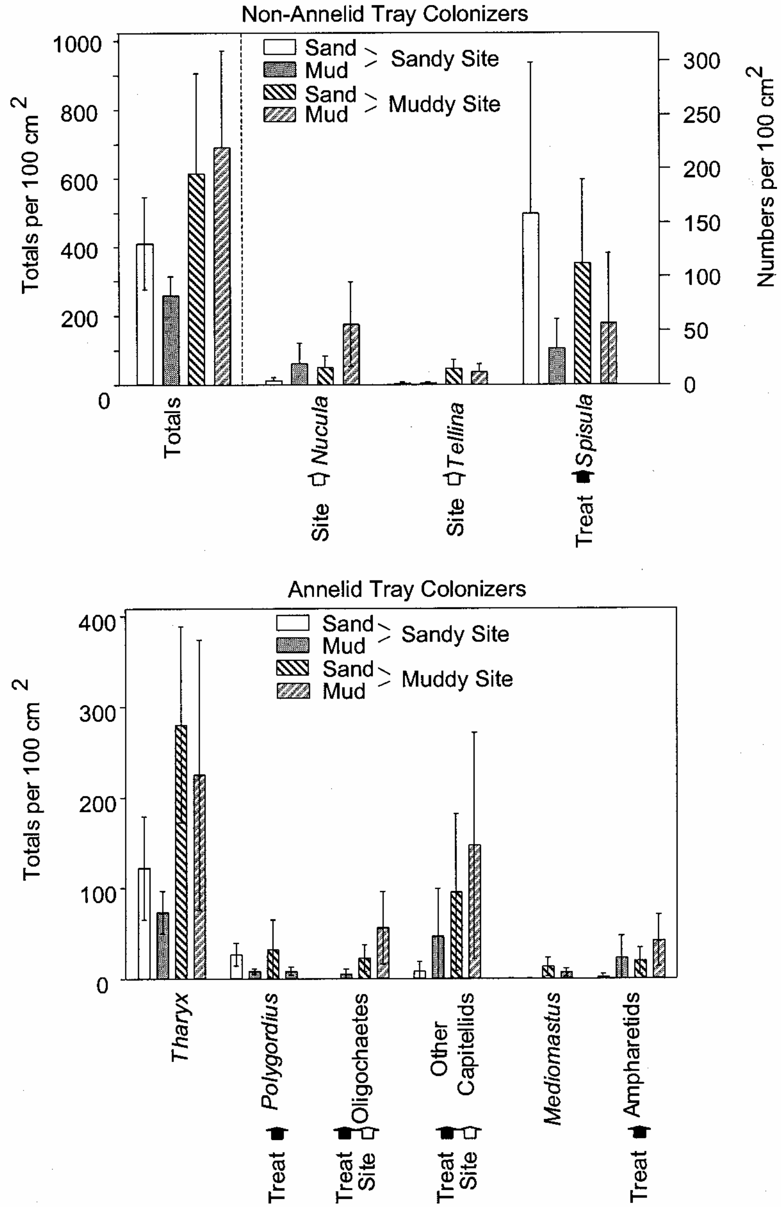

Figure 4. Means and 95% confidence intervals for non-annelid and annelid macrofauna in sediment trays. "Sand" and "Mud" refer to sand and mud sediment treatments, respectively. In upper panel, the right axis scale is applicable to all taxa to the right of the dashed line. Solid arrows labeled "treat" below plots indicate significant treatment effects, and open arrows labeled "site" indicate significant site effects. Where significant interaction terms indicated that treatment or site response was variable, arrows are not shown. Taxa shown are those that PCAH analyses indicated were important in describing structure in local community cores and sediment trays.

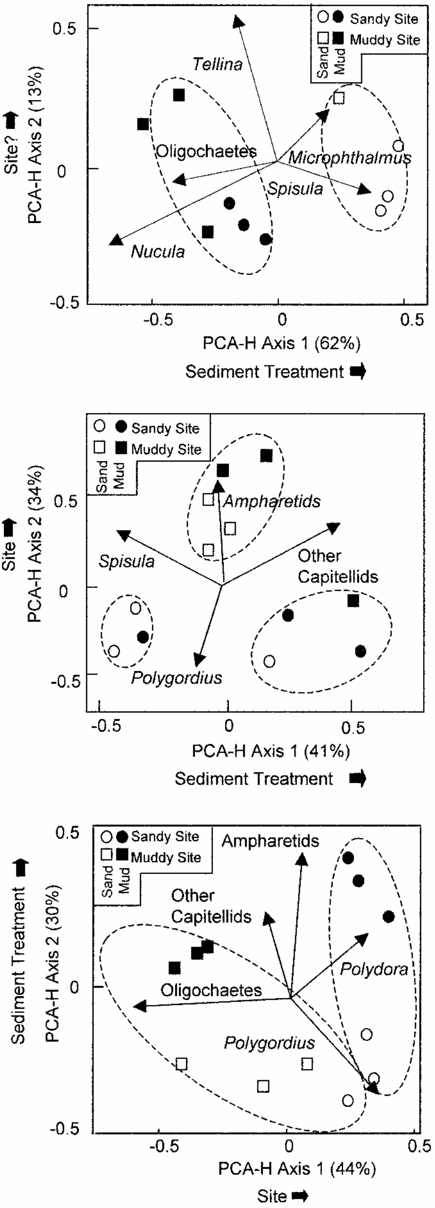

Figure 5. Metric scaling ordination in two dimensions of the spatial pattern of tray treatments based on CNESS dissimilarity with $m = 10$. Sand and mud refer to sediment treatments within sites. Percentages on axes denote variation explained by each of the principal components, and secondary axis labels denote interpreted meaning of the principal components. PCAH ordination species vectors have been overlaid on community ordination to describe which species drive spatial pattern. Dashed ovals indicate major groupings from cluster analysis. Top panel is 1–4 Aug. experiment, middle panel is 16–19 Aug experiment, and lower panel is 14–19 Sept experiment.

describing the muddy site, whereas *S. solidissima* and *Polygordius* sp. were important in describing the sandy site. Discriminant function analysis based on site indicated that the presence of ampharetid, capitellid, and several other polychaete taxa were important in differentiating muddy from sandy site trays (Table 1). The presence of *S. solidissima* and *Parougia caeca* were important in differentiating sandy from muddy site trays (Table 1).

In the 14–19 Sept. experiment, deployment site (corresponding to axis 1) and treatment (corresponding to axis 2) were both important in explaining colonization patterns (Fig. 5-bottom panel). *Polygordius* sp. in sand and ampharetids and capitellids in mud contributed to treatment differences, whereas oligochaetes at the muddy site and *Polydora cornuta* at the sandy site contributed to between-site differences. Discriminant function analysis also indicated that oligochaetes were important in distinguishing muddy from sandy site deployments, along with several polychaetes (Table 1). Ampharetids and capitellids contributed to mud treatments.

Rarefaction curves for tray experiments indicated that sediment treatment had no clear impact on diversity pattern but that deployment site did (Fig. 6). Treatments deployed at the sandy site were generally less diverse than those deployed at the muddy site. Shannon-Weiner diversity did not indicate any obvious pattern (for sandy site $\bar{x}_{\text{mud treatments}} = 1.6$, $se = 0.1$, $\bar{x}_{\text{sand treatments}} = 1.35$, $se = 0.1$, and for the muddy site $\bar{x}_{\text{mud treatments}} = 1.6$, $se = 0.1$, $\bar{x}_{\text{sand treatments}} = 1.7$, $se = 0.1$). An ANOVA comparison of Shannon-Weiner diversity did not indicate any significant difference in treatment ($F = 0.56$, $P = 0.46$), deployment site ($F = 1.6$, $P = 0.21$), or date ($F = 0.63$, $P = 0.54$). ANOVA analysis of $E(S_{100})$, however, indicated a significant site ($F = 4.95$, $P = 0.041$) and date ($F = 5.37$, $P = 0.010$) effect, but no treatment ($F = 0.02$, $P = 0.879$) effect. Species richness (muddy site $\bar{x}_{\text{sand treatments}} = 21.3$ species, $se = 0.8$, $\bar{x}_{\text{mud treatments}} = 18.9$ species, $se = 2.0$, sandy site site $\bar{x}_{\text{sand treatments}} = 15.0$ species, $se = 0.7$, $\bar{x}_{\text{mud treatments}} = 15.0$ species, $se = 1.3$) was significantly higher in trays deployed at the muddy site than the sandy site ($F = 13.29$, $P = 0.001$) and also differed by date ($F = 4.42$, $P = 0.021$), but treatment was not significant ($F = 0.889$, $P = 0.353$). Evenness was not significantly different in terms of treatment ($F = 1.17$, $P = 0.288$), site ($F = 0.03$, $P = 0.872$), or date ($F = 0.36$, $P = 0.703$).

4. Discussion

After many descriptive studies of pattern in benthic communities, there is still only a modest understanding of how pattern is maintained (e.g. Snelgrove and Butman, 1994). Physically dynamic environments tend to have reduced diversity relative to more benign habitats (Sanders, 1969; but see Thistle, 1983 for meiofauna), and extremely productive environments are often characterized by hypoxia and low diversity (Levin and Gage, 1998). Current thought on pattern determination can be largely divided into pre- (e.g. Snelgrove and Butman, 1994) and post-colonization (e.g. Ólafsson *et al.,* 1994) schools, but most workers agree that both kinds of processes can be important in different circumstances. We reported previously that habitat selection within sites in the LEO-15

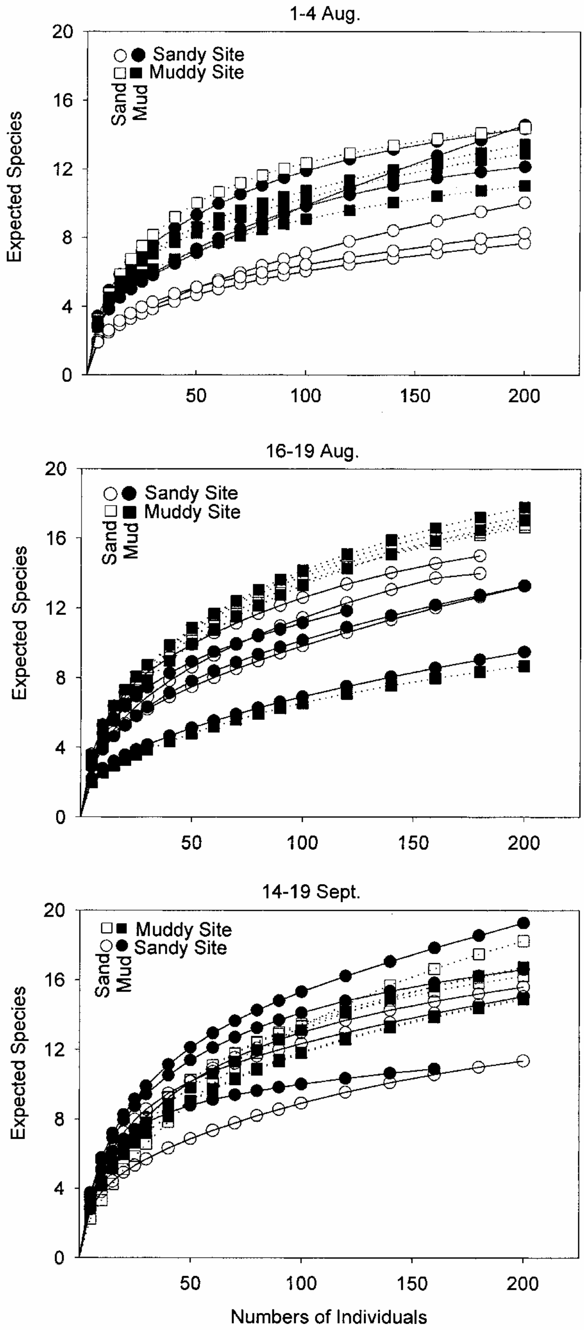

Figure 6. Rarefaction curves for each treatment at each site for each of the three experiments.

study area contributed significantly to initial pattern for several of the dominant taxa, although larval transport to the sites affected settlement intensity (Snelgrove *et al.,* 1999). Here we show that composition and diversity of sedimentary assemblages may be set at colonization.

In the local communities, *Nucula annulata, Mediomastus ambiseta,* oligochaetes, *Tharyx* spp., and a number of other polychaete taxa were important components of community structure at the muddy site, whereas *S. solidissima* and *Polygordius* sp. were important in describing the sandy site. Their importance is consistent with previous studies from this area (Garlo, 1980) and more extensive areas of the shelf (e.g. Boesch, 1979), which indicate similar sedimentary associations. What is interesting, however, is that many species important in describing local communities at the two sites were also important in describing colonization patterns.

Sediment treatment and deployment site were both important in explaining variation in colonizers. Their relative importance varied depending on larval selectivity and whether deployment date coincided with larval availability. *S. solidissima* dominated meroplankton samples during the first experiment, but was virtually absent in the last experiment (Ma, 1997; Snelgrove *et al.,* 1999); this pattern is consistent with peak July settlement of *S. solidissima* in the area (Ma, 1997; Weissberger, 1998). This result has been treated cautiously, however, because plankton samples were collected only once during each experiment. Nonetheless, *S. solidissima,* which has been shown to be selective in laboratory flume experiments (Snelgrove *et al.,* 1998), contributed to treatment differences when larvae appeared to be most abundant. *Tharyx* spp. contributed to site (but not treatment) differences in the second and third experiments when it was abundant. Other taxa, such as *Tellina* spp. and *Microphthalmus* spp., explained variance in colonization patterns but were unimportant in discriminating between treatment or site effects. Thus, they colonized both sites and did so nonselectively.

The majority of tray colonizers were recently settled larvae or small juveniles, and for most taxa it is uncertain whether colonization was achieved by settlement of planktonic larvae or post-settlement redistribution of juveniles. Based on shell size, we concluded that *S. solidissima* in the first experiment settled as larvae, but in later experiments the colonizers also included juveniles (Snelgrove *et al.,* 1999), which is consistent with other work demonstrating post-settlement selectivity in invertebrates (e.g., Olivier *et al.,* 1996). Published information on oligochaetes and their absence from plankton samples suggests that they colonized trays by migration or as bedload transport. The capitellids belong to the genera *Capitella* or *Capitomastus* and probably settled as lecithotrophic larvae. Both taxa nonetheless exhibited selectively with respect to sediment type (Snelgrove *et al.,* 1999) and contributed to treatment and site differences. Capitellids were important in describing the response in two of the experiments; however, the taxa that colonized the trays were not the same as those that were important in the local fauna; this finding is consistent with the opportunistic life history of some common capitellid species (Grassle and Grassle, 1974). Selectivity of some taxa for specific treatments, considered in concert with the fact that tray treatments could still be visually differentiated from one another by the end of experiments, suggests that colonization was not simply the result of local sediments and fauna being swept indiscriminately into trays. Nonetheless, this pattern does attest to the dynamic nature of the study sites and the importance of early post-settlement redistribution at LEO-15 on a local scale.

Between-date differences in tray composition could have been related to duration of experiments rather than differences in availability of colonizers, but the first two 3-d experiments produced different results in terms of which species were critical in describing treatment differences. The third experiment, which lasted five days, could have been affected by the longer deployment time, but the taxa that described variation in this experiment were the same as those in the shorter experiments. Thus, differences in colonizer supply appear to be a more likely explanation for the observed patterns than successional processes (e.g. McCall, 1997; Zajac and Whitlatch, 1982). Some studies on successional processes have found that species composition in experimental sediments differs markedly from the background community and changes over time (e.g. McCall, 1977; Arntz and Rumohr, 1982; Zajac and Whitlatch, 1982), in some instances through facilitation (e.g. Gallagher *et al.,* 1983). McCall (1997) noted in his Long Island Sound colonization study that over a 10-day period or greater, large numbers of larval opportunists colonized experimental trays but were not abundant in the ambient sediments, suggesting habitat selection. But most settlement studies have focused on recruitment rather than initial colonization, and many have elevated experimental sediments and thereby reduced the potential for juvenile and adult migration. In studies where isolation of experimental sediment from the surrounding community (e.g. Smith and Brumsickle, 1989) had been minimized (e.g. Gallagher *et al.,* 1983; Thrush *et al.,* 1991; Savidge and Taghon, 1988) there was often greater similarity in species composition between ambient fauna and colonizers, perhaps reflecting the contribution of bedload transport and adult migration through the sediment. That many studies with reduced sediment isolation have been conducted in dynamic areas may also contribute to this difference.

In evaluating how patterns of community structure are established, our analyses build on earlier field studies demonstrating that habitat selection (Günther, 1991; Snelgrove *et al.,* 1999), and spatial variation in larval supply (Cameron and Rumrill, 1982) can influence settlement patterns of individual species in a manner consistent with adult patterns. Our previous work on habitat selection by individual species of sedimentary invertebrates has demonstrated a coherence between field patterns and laboratory experimental results (e.g., Butman *et al.,* 1988; Snelgrove *et al.,* 1998) or field experimental results (Snelgrove, 1994; Snelgrove *et al.,* 1999), but the results reported here are the most direct evidence that patterns of initial colonization in some sedimentary communities may parallel local community composition and structure.

The pattern of higher diversity (species richness, $E(S_{100})$) in trays at the muddy site relative to the sandy site indicates between-site differences in initial colonization. Differ-

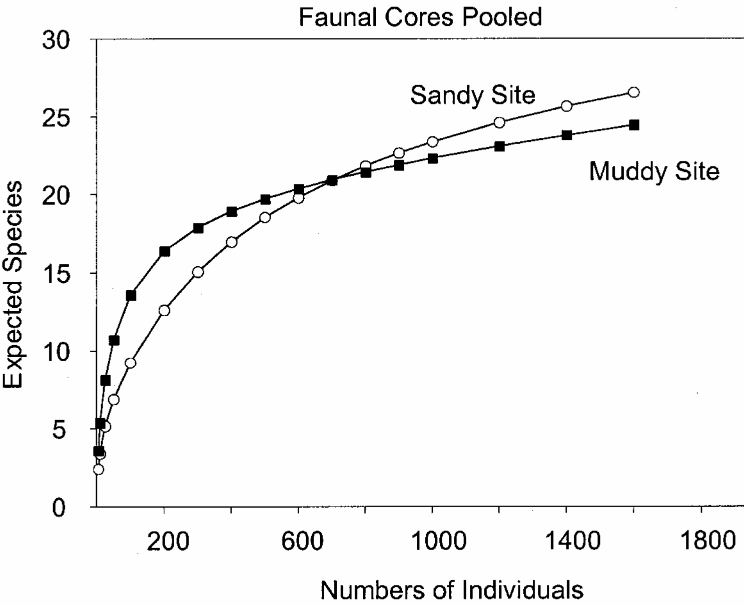

Figure 7. Rarefaction curves for local community samples where cores from each site have been pooled to produce a single curve.

ences in the supply of colonizers, which includes a local source of recently settled juveniles in addition to settling larvae, contribute to patterns of diversity in sedimentary fauna.

If ambient faunal cores from each site are pooled prior to rarefaction analysis, then the curves cross and the sandy site has a greater number of species for a given number of individuals (Fig. 7). Therefore, although the muddy site has more species in a small area (i.e., sample scale), there is probably a greater degree of patchiness in species composition at the sandy site, resulting in more species than at the muddy site at larger scales. This finding is consistent with diver visual observations that the sandy site was patchier in terms of visible fauna (R. Petrecca, pers. obs.). The present data provide an ambiguous result, and linking patterns in diversity of colonizers to those in the adult community may depend on the presence of clear diversity differences between sites on multiple scales, or a much better understanding of the scales of the patch structure in the different communities. Multiple short-term experiments could resolve the problem of temporal variability in larval supply and availability of post-settlement colonizers.

The experiments described here are useful in linking patterns of initial colonization to those in the local community. They suggest that habitat selection (by both larvae and post-settlement individuals), and to a lesser extent supply of post-settlement colonizers, both create patterns that are consistent with those in the local LEO-15 communities. In coastal New Jersey, post-settlement predation has a major impact on recruitment success of surfclams (Weissberger, 1989), and it is likely that other post-settlement processes such as active (Snelgrove *et al.,* 1999) and passive (e.g. Emerson and Grant, 1991) juvenile redistribution, predation disturbance (e.g. Ambrose, 1984) and juvenile mortality (Gosselin and Qian, 1997) contribute to patterns of some species at LEO-15. Nonetheless, the similarities in species composition of colonizers and local communities suggest that habitat selection and delivery of colonizers are important in setting patterns of composition. Our data are insufficient to link diversity in short-term experiments directly to the diversity in local communities, but they do indicate separate spatial and time-dependent determinants of diversity.

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