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In situ habitat selection by settling larvae of marine soft-sediment invertebrates

Abstract—To test whether larval selectivity at settlement contributes to distributional patterns of benthic infauna, we conducted three reciprocal sediment transplant experiments at 15-m-deep coarse-sand and muddy-sand sites (~3 km apart) on the continental shelf near Tuckerton, New Jersey. During 3- to 5-d deployments in 1994, larvae of the surfclam, *Spisula solidissima*, selected coarse sand over muddy sand, and capitellid polychaetes selected muddy sand over coarse sand, regardless of site. Thus, larvae of both taxa selected sediments typical of adult habitats, displaying selectivity consistent with previous flume experiments. Settlement intensity changed significantly over the ~6-week period during which experiments were conducted. Several other taxa exhibited selectivity consistent with field distributions, and several were nonselective. Significant site differences in settlement intensity were also observed on some dates for several taxa. Plankton pump samples taken at the sites during tray experiments suggested that significant differences in supply of surfclam larvae over the 3-km scale contributed to between-site differences in settlement. In the later experiments, surfclams in experimental trays were larger than would be expected for recent settlers, suggesting that postsettlement migration and selectivity occurred on small scales. These experiments demonstrate that differences in larval supply over scales of kilometers and time scales of weeks can affect settlement intensity but that habitat selection by settling larvae of some species of soft-sediment invertebrates may set initial distribution patterns.

Many studies have demonstrated spatially and temporally persistent sediment-associated patterns in marine benthos (reviewed by Snelgrove and Butman 1994), but the relative importance of larval supply and settlement in creating these patterns has been a subject of some debate (Butman 1987; Ólafsson et al. 1994; Snelgrove and Butman 1994). The potential importance of larval habitat selection was realized long ago in small-scale laboratory still-water experiments demonstrating that larvae delay or avoid settling in the absence of a particular sedimentary cue (e.g., Mortensen 1921). More recent laboratory flume experiments (e.g., Butman et al. 1988) have demonstrated that some species have the capacity for selectivity in realistic bottom flows. There is also evidence that small-scale flows affect initial settlement patterns (e.g., Eckman 1979; Butman and Grassle 1992; Snelgrove et al. 1993), and settlement therefore appears to be influenced by both behavioral and hydrodynamic processes.

Several field studies have documented a relationship between densities of settled juveniles and larval abundance in the water column (e.g., Muus 1973; Cameron and Rumrill 1982), but most studies have been done over time scales of weeks or longer, thus confounding larval supply and post-settlement processes. It is inarguable that processes such as

predation (e.g., Ambrose 1984), competition (e.g., Peterson 1977), and postsettlement redistribution (e.g., Emerson and Grant 1991) play important roles in structuring soft-sediment communities, but the potential importance of larval supply and habitat selection remains poorly known and is likely very important.

A key problem is that flume studies have focused on settlement, and field studies have focused on recruitment. Thus, the importance of habitat selection could not be inferred from field studies, and it is unknown whether laboratory studies can be extrapolated to the field (e.g., Schneider et al. 1997). In the present study, we performed short-term reciprocal sediment transplants between two sites with different sediment composition and faunas to evaluate how larval supply and habitat selection may contribute to observed patterns. The settlement of two taxa, for which we had previously conducted laboratory flume studies, allowed us to draw inferences on the applicability of flume studies to field situations.

Experiments were designed to determine the role of larval supply and selective behavior in establishing faunal distributions at the LEO-15 site (von Alt and Grassle 1992) on Beach Haven Ridge, a ~15-m-deep, 5-km-long by 1.5-km-wide ridge that is one of many such shore-oblique ridges along the coast of New Jersey. On the southern landward side of the ridge (39°27.69'N, 74°15.81'W) is a sandy habitat ($\phi \sim 1.0$, Craghan unpubl. data), in which the surfclam, *S. solidissima*, is an abundant and conspicuous component of the fauna. On the northern landward side of the ridge (39°29.29'N, 74°14.48'W) is a muddy-sand habitat ($\phi = 3.7$, Craghan unpubl. data) where polychaetes are dominant, and *S. solidissima* is rare. These sites will be referred to as the “sandy” and “muddy” sites, respectively.

Faunal composition at the two sites was determined from 7-cm-diameter cores (surface area = 38 cm²) pushed ~10 cm into the sediment by SCUBA divers in September 1994. Randomization of nine replicate cores was achieved using the hierarchical sampling approach of Morrissey et al. (1992). The bottom at the sandy site was rippled, so divers collected paired crest/trough samples rather than single cores, which resulted in a total of 18 samples. Samples were processed over a 300- μ m sieve, fixed in buffered 10% formalin, and transferred to 80% ethanol with Rose Bengal.

During the early summer of 1994, bulk sediment was collected from the sandy and muddy sites with a 0.04-m² Van Veen grab. The upper 2–3 cm of sediment was retained from multiple grabs, frozen, washed with fresh water, and pushed through a 1-mm sieve to remove shell fragments and large, dead invertebrates. These sediments were refrozen and later

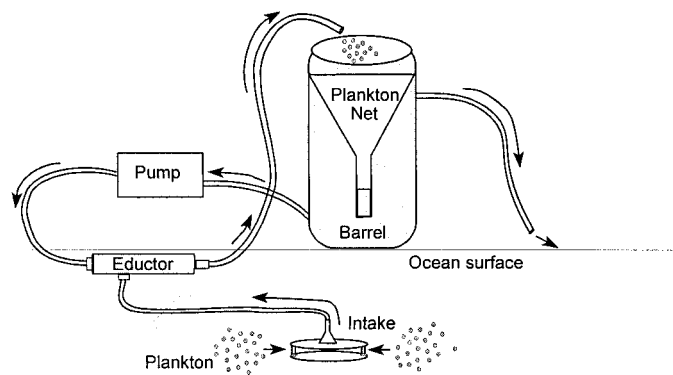


Fig. 1. Schematic diagram of plankton pump system used in the study. Water enters the intake, which consists of two 0.318-cm-thick parallel plates (30-cm diameter) separated by 2.54 cm, and passes through a 10-cm opening in the top plate, then through a 3.8-cm-diameter hose to an eductor, where it is combined with flow from a pump. The pump flow creates a negative pressure, causing water to flow upward from the intake, allowing collection of a sample in which organisms do not actually pass through the pump. Water flows from the eductor through a 7.6-cm-diameter hose and into a 102- μm mesh net in a large barrel. From the barrel, the filtered water flows through a 5.1-cm-diameter hose back to the pump, creating a loop that is closed except for seawater entering through the intake. A pumping rate of ~ 90 liters min^{-1} , in conjunction with a hydrodynamically designed intake, minimizes disturbance to flow streamlines that might result in larval avoidance behavior and subsequent undersampling.

thawed and used in reciprocal sediment transplants at the sandy and muddy sites. On each of three different dates (1 August, 16 August, and 14 September 1994), replicates of hydrodynamically unbiased trays (described by Snelgrove 1993) were filled with defaunated sand or mud from the respective sites, resulting in a sediment surface area of 100 cm^2 and 2-cm depth. Three replicates of each of the two types of sediment trays were sealed with lids and carried to the bottom by SCUBA divers, who placed them flush with the ambient seafloor at each site before removing the lids. Treatments were haphazardly interspersed along a 10-m transect perpendicular to the dominant tidal flow. Trays were left in situ for 3–5 d, depending on the deployment date, before divers placed sealing lids on the trays and carried them to the surface, where they were processed over a 100- μm sieve and preserved in buffered 4% formaldehyde.

One day during each tray deployment, duplicate, 500-liter plankton samples were collected from the sandy and muddy sites. An additional plankton sampling station was established at a site 3 km offshore of the sandy site (hereafter referred to as “offshore sand”). Sampling was achieved with a shipboard pumping system, which allowed sample collec-

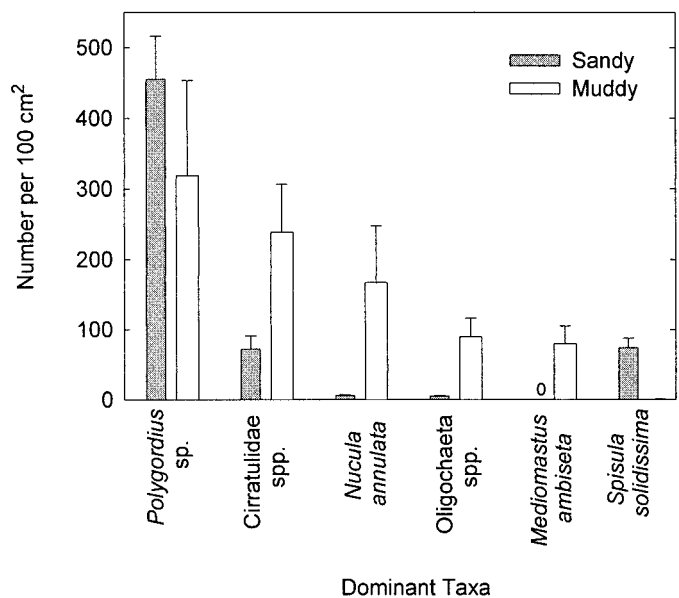
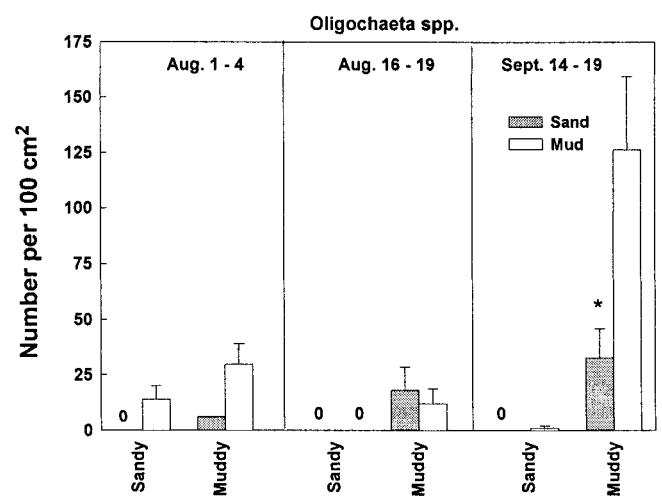
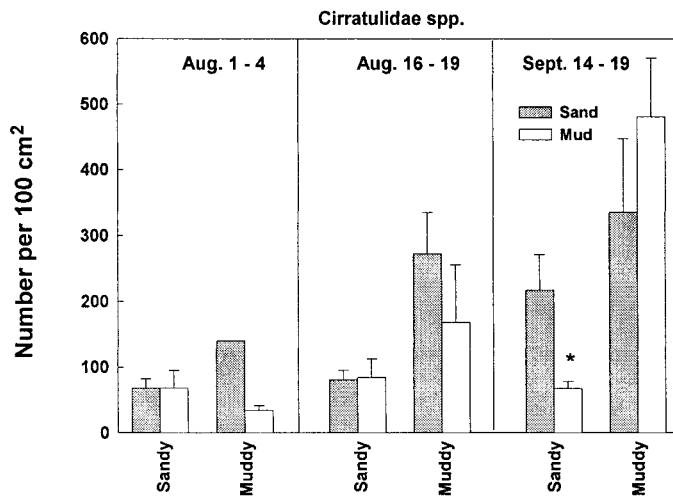
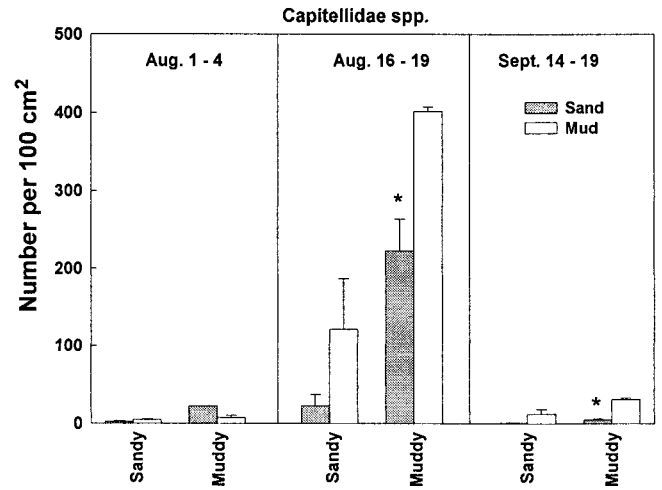
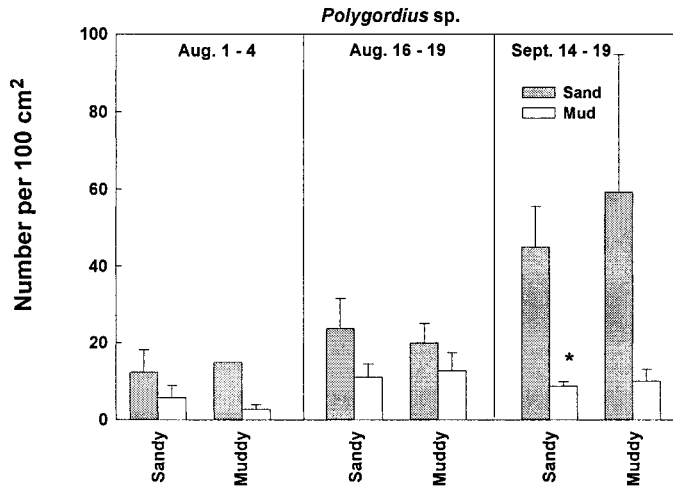
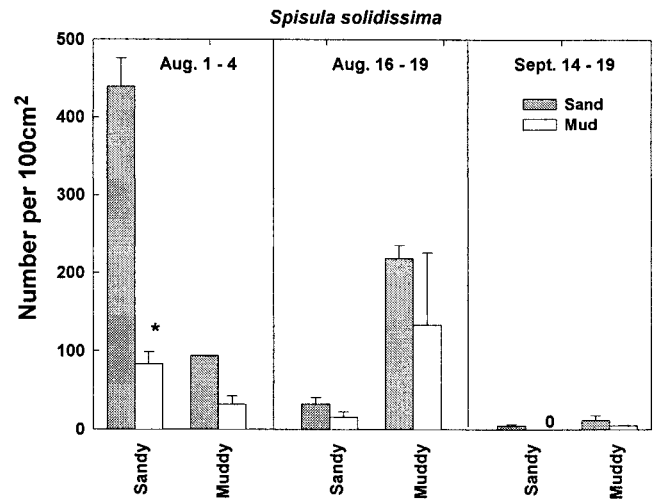
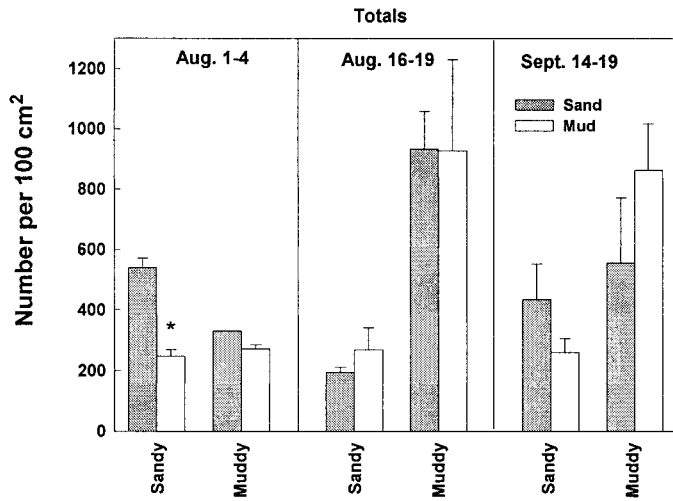


Fig. 2. Comparison of numbers of individuals of abundant organisms in ambient sediments at the muddy ($n = 9$) and sandy LEO-15 ($n = 18$) sites. Bar shading refers to sites where cores were collected. Bars denote means, and lines denote 1 SE.

tion without passing the meroplankton through the pump itself (Fig. 1). The shipboard system sampled through an intake that was either lowered to 1 m below the ocean surface or carried to the bottom by divers and placed so that the intake was approximately 5 cm above the sediment surface (Fig. 1). Water samples were filtered through a 102- μm net to retain larval polychaetes and bivalves, which were preserved for later enumeration.

Tray and plankton samples were transferred to 80% ethanol and stained with Rose Bengal within ~ 1 week of collection. Organisms were enumerated under a dissecting microscope and identified to the lowest possible taxonomic level. For the polychaetes in the tray and plankton samples, this was generally limited to the family level because individuals were extremely small and immature. At least three cirratulid species are known from the region, and we believe that the capitellids also include more than one species. We were unable to differentiate such small individuals to species with certainty. Capitellid polychaetes were members of the genera *Capitella* or *Capitomastus*, but more precise identification was not possible. Molluscs could generally be identified to species. For the faunal core samples, most individuals were identified to the genus or species level, although several groups such as cirratulid polychaetes were problematic and were therefore identified only to the family level.

Fig. 3. Densities of organisms recovered in trays for each deployment. Bar shadings refer to sediment treatments, with shaded bars denoting sand treatments and open bars denoting mud treatments. ANOVA of $\log(x + 1)$ -transformed data indicated overall significant treatment effects for *S. solidissima*, Capitellidae spp., and *Polygordius* sp.; modified models resulting from significant interaction terms involving treatment indicated significant treatment effects for Cirratulidae spp. as well. Asterisks indicate significant differences in within-experiment and site ANOVA comparisons. See text regarding site and date effects. All comparisons are based on three replicates, except the 4 August sand treatment at the sandy site, where only one tray was successfully recovered.



Deployment Sites

Deployment Sites

For the purposes of comparing faunas at the two sites, this level of resolution appeared to be adequate, and this was also greater resolution than we were able to achieve for tray samples.

Settlement data were analyzed using the analysis of variance (ANOVA) model $y = \mu + \text{date} + \text{site} + \text{treatment} + \text{date} \times \text{treatment} + \text{site} \times \text{treatment} + \text{date} \times \text{site} + \text{date} \times \text{site} \times \text{treatment} + \text{error}$, where μ is a constant, "date" refers to deployment date, "site" refers to deployment location (sandy or muddy site), and "treatment" refers to sediment treatment (sand or mud). Site and treatment were treated as fixed variables, and date was treated as random. Data were $\log(x + 1)$ transformed to homogenize variances for analyses. In instances where interaction terms were nonsignificant, they were dropped, and analysis was repeated.

Individual *S. solidissima* were measured for shell length using a color camera linking a Zeiss dissecting microscope to a Macintosh computer and monitor. The software program IMAGE® was then used to measure individuals after calibration with a stage micrometer. In samples where many individuals were present, the vial was rinsed into a petri dish, and the first 50 individuals observed were measured. Where <50 were present, all individuals were measured. Preliminary analysis indicated serious problems with heteroscedasticity that could not be resolved by data transformation; size was therefore compared among dates with a Kruskal–Wallis test.

Of the taxa abundant in trays, only *S. solidissima* larvae were abundant in plankton samples, and plankton analysis was therefore limited to this species. Thus, *S. solidissima* plankton abundance was analyzed using the ANOVA model $y = \mu + \text{date} + \text{site} + \text{depth} + \text{depth} \times \text{site} + \text{depth} \times \text{date} + \text{site} \times \text{date} + \text{depth} \times \text{site} \times \text{date} + \text{error}$, where μ is a constant, "date" refers to sampling date, "site" refers to deployment location (muddy, sandy, or offshore site), and "depth" refers to surface or bottom samples. Depth and site were treated as fixed, and date was treated as random; because of heteroscedasticity of variances, data were $\log(x + 1)$ transformed.

The archiannelid, *Polygordius* sp., and to a lesser extent the cirratulids, were the dominant taxa in the ambient macrofauna in sediments at both sites (Fig. 2). Most of the other abundant species were common at only one of the two sites. A mixture of other taxa dominated the muddy site, including *Nucula annulata*, *Oligochaeta*, and *Mediomastus ambiseta*. *S. solidissima* was abundant at the sandy site but absent from the muddy site; although the core size used only sampled small surfclams effectively, divers routinely collected large individuals from the sandy site but never observed them at the muddy site.

For the surfclam, *S. solidissima*, settlement was significantly higher in sand relative to mud treatments ($F = 73.52$, $P = 0.01$), and a significant date \times site effect ($F = 39.26$, $P = 0.02$) was also observed. The significant interaction term likely reflects higher settlement at the sandy site during the 1–4 August experiment and higher settlement at the muddy site during the 16–19 August experiment (Fig. 3). Settlement was low at both sites in the 14–19 September experiment. Previous laboratory flume experiments have shown that *S. solidissima* larvae select sand over mud (Snel-

grove et al. 1998), and this finding is consistent with field observations of adult distributions (reviewed by Yancey and Welch 1968). This field demonstration of preferential settlement of *S. solidissima* in sand shows that flume experiments may be extrapolated to nature and that habitat selection likely plays a role in *S. solidissima* distributions.

Plankton pump samples exhibited a number of different patterns of *S. solidissima* abundance, depending on depth and date, but several patterns were particularly striking (Fig. 4). First, significant date ($F = 7.15$, $P = 0.03$), depth \times site ($F = 10.82$, $P = 0.02$), and date \times site ($F = 12.42$, $P = 0.02$) effects were observed. Significantly higher numbers of *S. solidissima* were observed in bottom samples from the sandy site than in bottom samples from the muddy site on 3 August, a pattern consistent with tray results. On 17 August, bottom sample numbers were higher for the muddy site than for the sandy site, and surface samples had significantly higher abundance at the muddy site compared to the sandy site; densities in trays during this period showed a similar pattern. During the third deployment, very low larval densities were observed at both sites, and settlement in trays was also extremely low. These larval distribution patterns correspond well with settlement patterns in trays, suggesting that differences in supply exist, even within the ~3-km scale separating the two experimental sites, and that these differences affect patterns of settlement. This correspondence between supply and settlement may simply be coincident given that plankton samples were only taken at one time during each of the sediment deployments, but the pattern is intriguing. In conjunction with tray results, it suggests that broad-scale supply and settlement intensity, even over spatial scales of ~3 km, are largely a function of circulation and passive transport but that habitat selection also plays a significant role.

Comparisons of shell lengths of settled *S. solidissima* indicated significant differences in size distribution with date (Kruskal–Wallis $\chi^2 = 419.2$, $P = 0.00$). Smaller individuals were observed in the first experiment compared with those in the 16–19 August and 14–19 September experiments (Fig. 5), being within the expected range for very recent settlers based on our laboratory experience (Snelgrove et al. 1998). The sizes of many individuals in the second and third deployments suggested that they were recently settled juveniles that migrated in from the surrounding sediments. This is consistent with observations that juvenile surfclams are highly active, that they "jump" around on the ocean bottom (Snelgrove unpubl. data), and that this behavior, combined with bedload transport, may have carried some individuals into the trays. The size differences among experiments suggest that habitat selection in *S. solidissima* may be achieved either at larval settlement or by recently settled juveniles.

Settlement of the capitellid polychaetes was significantly higher in mud than in sand ($F = 6.49$, $P = 0.02$). Significant date ($F = 28.60$, $P = 0.00$) and site ($F = 17.63$, $P = 0.00$) effects were also observed, likely reflecting high settlement during the 16–19 August experiment and higher settlement at the muddy site than at the sandy site. The morphology of the recently settled Capitellidae spp. suggested that the larvae were lecithotrophic, akin to those of *Capitella* spp. I and II, which were previously used in flume experiments show-

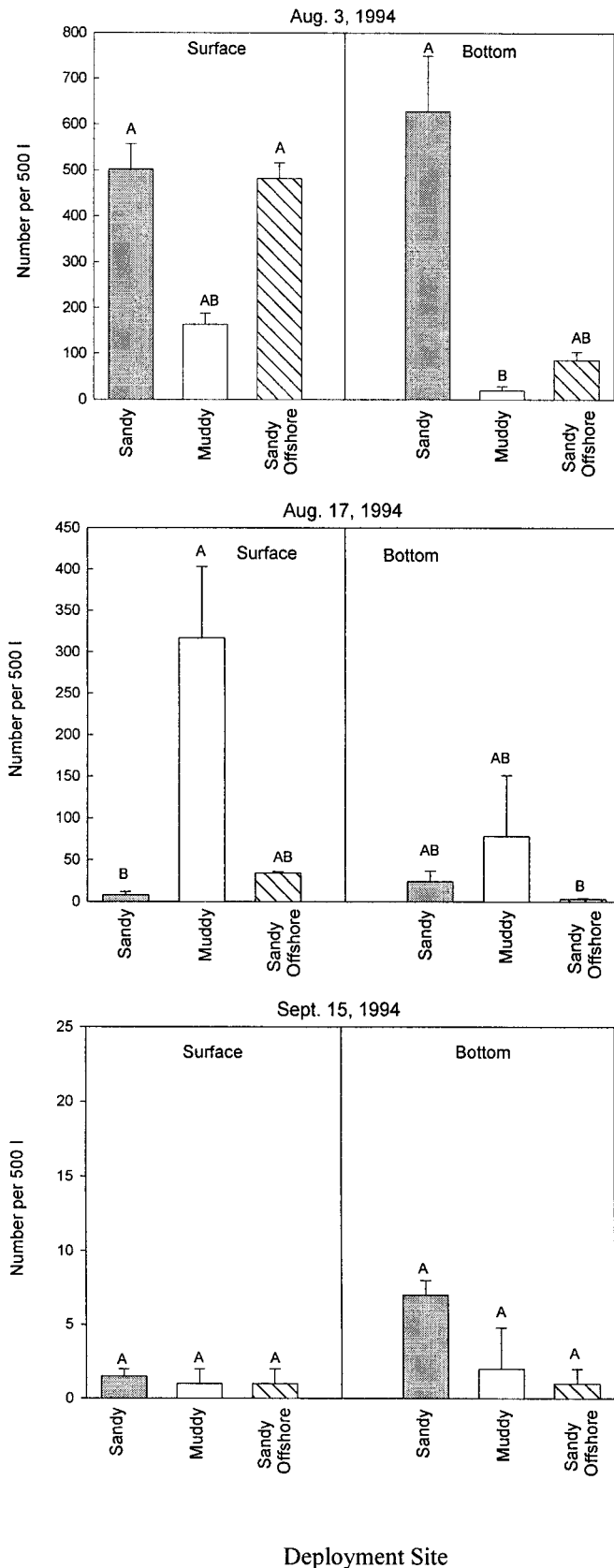


Fig. 4. Densities of planktonic *S. solidissima* collected in surface and bottom samples during tray deployments at the sandy and

ing their significant preference for mud over sediments low in organic matter (Butman et al. 1988; Grassle and Butman 1989; Butman and Grassle 1992; Grassle et al. 1992). Such a preference is consistent with distributions of natural populations (Grassle and Grassle 1978). Lecithotrophic capitellid larvae were absent from the plankton pump samples, suggesting that sampling missed these highly selective larvae (cf. Graham and Sebens 1996).

Polygordius sp. settled in significantly higher numbers in sand than in mud treatments ($F = 20.34$, $P = 0.00$) and depended on date ($F = 8.17$, $P = 0.002$), but the site effect was not significant. Oligochaeta spp. settled in significantly higher numbers in mud than in sand treatments ($F = 4.25$, $P = 0.05$), and significant site ($F = 56.68$, $P = 0.00$) and date ($F = 3.80$, $P = 0.03$) effects were also observed. Corresponding flume experiments have not been done for *Polygordius* sp. or any marine oligochaetes, but sediment choices exhibited by these taxa were consistent with ambient distribution patterns (Fig. 2). As with the Capitellidae, these taxa were generally absent from plankton pump samples. A significant date \times site \times treatment interaction term for Cirratulidae ($F = 6.12$, $P = 0.01$) indicated that different patterns were observed on different dates (Fig. 3). Indeed, no consistent patterns were observed with cirratulids, but this apparent lack of selectivity may be a result of our inability to identify individuals to species, or it may reflect nonselective settlement.

A significant date effect was observed for many taxa, indicating that even over the relatively short time scale of these experiments, larval settlement may change rapidly. This finding is consistent with previous work indicating rapid temporal change in larval supply (Levin 1986) and settlement (Luckenbach 1984). Even though the first two deployments were within a 2-week period, abundance and composition of settlers changed markedly (Fig. 3). At Beach Haven Ridge, these differences may be related to changes in oceanographic conditions, particularly with respect to upwelling (Glenn et al. 1996). The 1–4 August deployment corresponded to the relaxation of a major upwelling event along the New Jersey coast (Glenn pers. comm.), whereas the other experiments were deployed during nonupwelling periods. Specifically how this 1994 event might have contributed to the observed differences can not be discerned, but intensive plankton sampling at the LEO-15 sites in the summers of 1995–1997 suggests a relationship between upwelling relaxation and discrete pulses of *S. solidissima* larvae (Ma 1997). Such transitory transport events would be consistent with the rapid change in abundances of different taxa over the ~6 weeks during which the experiments were done. Patchiness in larval supply was one of several possible explanations invoked for patchy age structure in *Spisula*

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muddy stations and at an offshore station. Bar shading denotes sites where pump collector was deployed, with shaded bars denoting the sandy site, open bars denoting the muddy site, and hatched bars denoting the offshore site. Means (± 1 SE) are based on duplicate samples. Within each date, bars with the same letters (A, B, or C) above them are not significantly different.

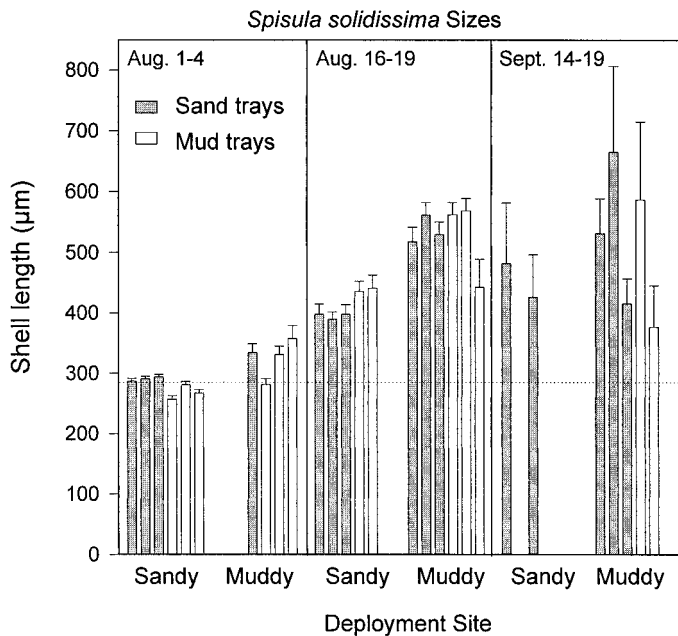


Fig. 5. Mean (± 1 SE) for shell length distribution of *S. solidissima* in each replicate for sediment tray experiments. Bar shading denotes tray treatment from which individuals were collected, with shaded bars denoting sand trays and open bars denoting mud trays. Most means are based on a random subsample of 50 individuals; however, the densities in the September deployment were very low, and means are sometimes based on as few as five individuals or, in a few instances, are missing. The dotted line indicates the average shell length for recently settled, laboratory-reared *S. solidissima* (Snelgrove et al. 1998).

ovalis populations in coastal France (David et al. 1997), and the association of larvae of other taxa with transitory features such as upwelling fronts (e.g., Roughgarden et al. 1988) and internal waves (Shanks 1986) has previously been noted.

Of the five abundant taxa in experimental sediments, four were selective with respect to sediment type (Fig. 3), and selectivity was consistent with respect to adult distributions (Fig. 2). Thus, selective behavior of settling larvae of infauna appears to contribute to natural distribution patterns. Numbers of settlers within sites also corresponded well with observed ambient faunal densities (i.e., sites with high abundance of adults of a given taxon tended to have higher total numbers of settlers of that taxon). The obvious exceptions were the Capitellidae spp. This may relate to a fundamental difference between planktotrophic and lecithotrophic species, especially when the latter are highly habitat selective. One might expect to find a correspondence between water-column abundance and settlement in the former but not the latter.

These data provide the first evidence for in situ habitat selection by soft-sediment infaunal larvae, indicating that although larval delivery to a particular habitat is largely a function of physical processes, habitat selection plays an important role in determining patterns of initial settlement and distribution. This finding is consistent with flume studies at smaller scales (e.g., Butman et al. 1988; Grassle and Butman

1989; Butman and Grassle 1992; Snelgrove et al. 1993), suggesting that experimental flume studies have applicability to field patterns. The specific aspect(s) of the two sediment treatments that resulted in preferential larval settlement are not known, but organic content (Butman et al. 1988; Grassle and Butman 1989) and biogeochemical compounds (Woodin et al. 1993) have been suggested as potentially important positive and negative cues. There is little doubt that post-settlement variables such as predation play a major role in the population dynamics of some species at LEO-15, and this is particularly true for surfclams, which suffer extremely high predation mortality soon after settlement (Garlo 1982; Weissberger 1998).

But do these findings tell us anything about whether realistic flow is actually needed to evaluate larval settlement in laboratory experiments, given that higher settlement at slack tide has been observed for several taxa (Whitlatch and Osman 1998 and references therein)? Current meter data from the sandy site indicate that weak flows are extremely rare; particularly when wave energy is considered, shear velocities less than the 0.3 cm s^{-1} used in our previous flume experiments are rarely observed (Glenn pers. comm.). Given that habitat selection was observed for *S. solidissima* in field experiments and was observed consistently in laboratory flume flow but not in still-water experiments (Snelgrove et al. 1998), it would seem that flume flow experiments provide an outcome more representative of field results than still-water experiments, at least for this species.

The consistency between our experimental results and natural faunal patterns suggests that for *S. solidissima* and other taxa at LEO-15, larval supply and habitat selection probably both play significant roles in determining temporal and spatial variability in faunal patterns. Broad-scale supply and mesoscale physical features determine whether larvae actually encounter a given habitat, and multiple taxa appear to be able to choose or reject a particular sediment attribute once in that habitat. The scale at which the relative importance of these processes may change and the importance of ambient flow conditions in this transition remain to be tested.

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