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Mechanisms of infaunal polychaete dispersal and colonization in an intertidal sandflat

by David H. Shull^{1,2}

ABSTRACT

Changes in benthic infaunal population densities following disturbance may be influenced by colonization mechanisms. Accordingly, this study experimentally examined the relative importance of four colonization mechanisms for seven numerically dominant polychaete species in an intertidal estuarine sandflat in Connecticut, USA. The colonization mechanism an organism used depended upon species characteristics including larval developmental mode and depth distribution within the sediment. A spionid polychaete with planktonic larval development, *Polydora cornuta*, colonized experimental disturbance treatments primarily by larval settlement. A surface-dwelling syllid polychaete with nonplanktonic development, *Streptosyllis arenae*, colonized mainly by bedload transport. Two syllid polychaetes developmentally and morphologically similar to *S. arenae*, yet deeper dwelling, colonized by different mechanisms than *S. arenae*. *Parapionosyllis longicirrata* colonized primarily by burrowing and *Brania wellfleetensis* colonized by both burrowing and bedload transport. Two other species with nonplanktonic development, *Pygospio elegans*, and *Nereis acuminata*, colonized by bedload transport and by burrowing. The more vagile *Nereis* also colonized by post-larval swimming. Members of the well-known opportunistic sibling species, *Capitella*, colonized by larval settlement, burrowing and by bedload transport. Although all species were dispersed during sediment transport events at the study site, this transport mechanism appeared to control colonization rate for only the small surface-dwelling species, *S. arenae*.

Colonization mechanisms influenced temporal changes in colonization rates for these species. Colonization rate for *P. cornuta* was highest during the period of peak larval production. Colonization rate for *S. arenae* was positively correlated with sediment transport rate. Seasonal changes in colonization mechanisms were also observed. Burrowing and bedload transport were relatively more important colonization mechanisms in autumn when rates of larval settlement and post-larval swimming were low. This study demonstrated that temporal changes in colonization rates for some species could be understood if the primary colonization mechanism was determined.

1. Introduction

Small-scale disturbances (e.g., pits and mounds created by the feeding and burrowing activities of animals) are common in intertidal and subtidal soft-sediment habitats (e.g., Reidenauer and Thistle, 1981; VanBlaricom, 1982; Levin, 1984). Although one would expect intuitively that early colonists would possess characteristics that aid in rapid

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dispersal, early colonists of small-scale soft-bottom disturbances are often brooders exhibiting life history characteristics which limit larval dispersal, such as a short or nonexistent planktonic stage (McCall, 1977; Levin, 1984). The reason for these characteristics may be related to the small size of colonists or the relative abundance of benthic and pelagic predators (Vance, 1973; Strathmann and Strathmann, 1982; Levin, 1984). However, this observation raises the question; what dispersal mechanisms do infaunal species with an abbreviated or nonexistent planktonic larval stage use to colonize recently disturbed patches of sediment?

Colonization mechanisms found to occur in marine soft-bottom habitats include larval settlement (Dauer and Simon, 1976; Santos and Simon, 1980), burrowing (Smith and Brumsickle, 1989; Kukert and Smith, 1992), erosion of organisms from surrounding sediments (Savidge and Taghon, 1988; Emerson and Grant, 1991), and swimming by post-larvae (Levin, 1984; Butman, 1987). The purpose of this study was to investigate the relative importance of these four potential mechanisms for the colonization of defaunated sediments by infaunal polychaetes inhabiting a sandflat. This information was then used to formulate and test the hypothesis that colonization rate should be positively correlated with sediment transport rate for species which colonize by erosion from surrounding sediments.

Determining the relative importance of colonization mechanisms used by infaunal species is critical for predicting changes in benthic community structure following a disturbance (Santos and Simon, 1980; Levin, 1984; Smith and Brumsickle, 1989). Because some colonization mechanisms transport specific life-history stages of species, colonization mechanisms will likely affect the age-structure of colonist populations which may further influence colonist population dynamics (Zajac and Whitlatch, 1991) and biotic interactions within recently disturbed patches (Woodin, 1976; Probert, 1984). In addition, the relative importance of colonization mechanisms will influence how colonization rate will be affected by characteristics of the disturbed area, such as timing or patch size of disturbance, and characteristics of the environment, such as flow velocity or sediment-transport rate.

2. Materials and methods

a. Study site

Experiments were conducted in the lower intertidal zone of a sandflat near the mouth of the Poquonock River in Groton, Connecticut (41°19'15"N, 72°02'40"W, Fig. 1). The study area was protected from the wind on all sides. However, currents during spring tides were of sufficient magnitude to cause sediment transport at this site. Measurements of ripples (approximately 8-cm in length, 1-cm height) and the distribution of painted sediment particles deployed at the site indicated that sediment transport reworked the top 1 cm of the bed. Sediment was composed of medium sand (median grain diameter between 250 and 500 μm) with less than 0.5% silt-clay ($<63 \mu\text{m}$), and 0.5% organic matter (ash-free dry weight). Water temperature and salinity at low tide ranged from 19°C to 23°C and 16 p.s.u. to 26 p.s.u. (practical salinity units) during the study period.

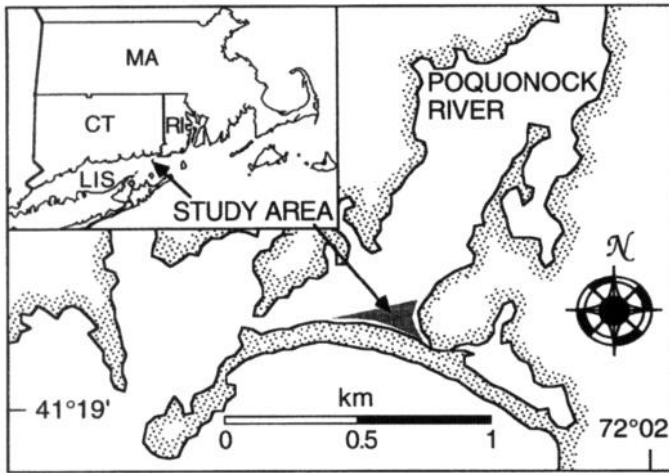


Figure 1. Study site located in the lower intertidal zone of a sand-flat near the mouth of the Poquonock River, Groton, CT. Densely stippled region shows the areal extent of the sandflat.

The most obvious small-scale disturbances at the site were feeding pits made by gulls and possibly other intertidal predators (e.g., crabs, horseshoe crabs). The pits ranged in size from about 8 to 30 cm in diameter with a median size of 15 cm. The depth of the pits averaged 3.7 cm (± 0.9 , 95% C.I.). The pits were distributed in clusters across the sandflat as seagulls were observed to feed in groups. Within a patch of pits, the average density was roughly 7 pits \cdot m⁻². Larger pits made by clam diggers (approximately 1-m in diameter) were sometimes observed. A pilot study was conducted from May 31, 1990 until June 5, 1990 to determine community composition, infaunal vertical distributions, to test experimental disturbance and dispersal trap designs and to estimate colonization rates of azoic sediments (details given in Shull, 1992).

b. June colonization experiment

The purpose of this experiment was to determine the relative importance of four colonization mechanisms: larval settlement, burrowing, bedload transport and post-larval swimming. These colonization mechanisms were defined as follows. Colonization by larval settlement was defined as arrival of larvae at the surface of a sediment patch and subsequent metamorphosis. Individual colonists were considered to have colonized by this mechanism if the sizes of individuals found in experimentally disturbed areas were within the size range of recently settled individuals. Burrowing was defined as movement through sediments and was considered to occur during this study if organisms colonized defaunated sediments which were modified to only allow entry below the sediment surface. Colonization by erosion from surrounding sediments was considered a process which delivered post-larval colonists to the surface of a defaunated area during sediment transport. Colonization by this mechanism was termed bedload transport because it appeared as

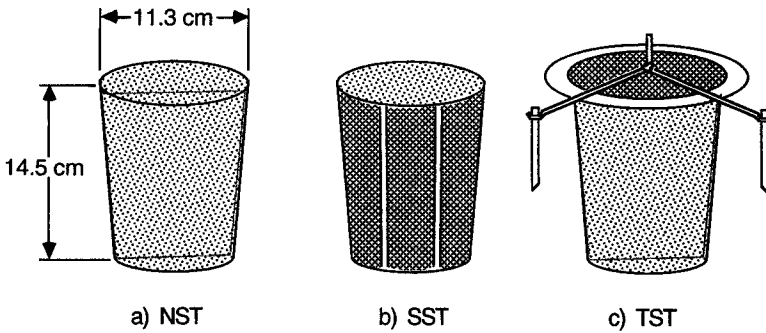


Figure 2. Disturbance Treatments. (a) 11.3-cm diameter plug of freeze-thawed sediment with no mesh acting as a control (NST). (b) Sediment plug with 150- μ m mesh down the sides (SST). (c) Sediment plug with 150- μ m mesh on top (TST).

though most transported individuals maintained close proximity to the bed. It is recognized, however, that this dispersal mechanism may include suspended transport as a component. Colonization by post-larval swimming was defined as arrival of juveniles and adults which had previously actively entered the water column.

To determine if colonization occurred by burrowing or from the sediment surface, three colonization treatments were deployed at the study site (Fig. 2). These consisted of defaunated sediment plugs: (a) without mesh barriers (hereafter referred to as no-screen treatment or NST), (b) enclosed by a plastic barrier along the bottom and a mesh side barrier (side-screen treatment or SST) and (c) with a mesh barrier on top (top-screen treatment or TST). Sediment plugs were created by collecting intact sediment cores from the study area adjacent to the experimental site and freezing them for more than one week in 1150-ml plastic beakers (11.3 cm top diameter, 9 cm bottom diameter, 14.5 cm height) to kill all macrofauna.

The NST consisted of intact freeze-thawed plugs of sediment which were removed from the beakers and placed surface side up into excavated holes so that they were flush with the sediment surface. This treatment allowed colonization by all mechanisms and acted as a disturbance control. For the SST, sediment was frozen and thawed in plastic beakers in which four side panels (6 \times 11 cm) had been cut out and replaced with 150- μ m mesh which was attached with silicone aquarium glue. This treatment was designed to exclude burrowing macrofauna. The final treatment (TST) was a sediment plug covered at the surface of the bed by 150- μ m mesh. The mesh was held in place by a plastic ring (12.5-cm inner diameter, 18-cm outer diameter) which was secured to the bed by three 9-mm diameter wooden pegs attached to the ring by nylon line and inserted into the sediment. This treatment was designed to exclude colonization from the sediment surface and water column.

Treatments were located using 9-mm diameter wooden pegs, 30-cm in length. Pegs were inserted until they were nearly flush with the bed on either side of the defaunated sediment

plugs, 28 cm from the plug center and on a line perpendicular to the direction of current flow.

Replicates ($n = 15$) of each treatment were assigned random locations in a 9- by 15-m rectangular array. The distance between each replicate was 1.5 m. The array of treatments was aligned so that disturbed patches were not directly in line with one another relative to the direction of current flow. This was done to minimize potential current induced row or column effects. Also, during deployment, kneeling boards were used to minimize disturbance to the sandflat in the vicinity of the experiments.

The experiment was carried out from June 21 to July 11, 1990, during the period of peak reproduction for many species in this area (Dobbs, 1981; Zajac and Whitlatch, 1982; personal observation). Five randomly chosen replicates of each treatment were (destructively) sampled after 5, 10, and 20 days using a 6-cm diameter core from the center of the disturbed patches. For the TST, the mesh ring was located and removed before coring. Cores were returned to the lab and sectioned into 0- to 1-cm, 1- to 4-cm and 4- to 10-cm depth intervals. Each section was preserved in 10% buffered formalin and later transferred into 70% ethanol and stained with rose bengal. Samples were sieved through nested 500- μm and 125- μm screens. The entire 500- μm fraction was sorted under a dissecting microscope. Organisms in the 125- μm fraction were floated off the sediment by repeated washings in a shallow pan before sorting. Five residues of the floating procedure were sorted to determine organism recovery efficiency. Recovery efficiency was 100% for all species included in this study. Because the naturally occurring feeding pits were only about 4-cm deep, and because the species of interest at the site were distributed primarily in the top 4 cm (see section on vertical distribution) only animals in the top 4 cm of the cores were enumerated.

Unfortunately, the glue holding the mesh of the TST failed and the mesh became detached from many of the plastic rings prior to the first sampling date. Therefore, although the TST disturbances were sampled, those data were not included in the analysis for the June colonization experiment.

The NST, SST and TST treatments were designed to distinguish between burrowing and surface colonization by preventing colonization by one of these mechanisms. Significantly lower densities of a species in the SST compared to the NST would indicate burrowing was the primary colonization mechanism. Significantly lower densities in the TST, relative to the NST, would indicate that colonization occurred from the sediment surface (e.g., larval settlement, dispersal by sediment transport). No significant differences between all treatments would indicate that colonization occurred by burrowing and from the sediment surface. Because no hydrodynamically unbiased treatments could be developed to directly test the relative importance of three components of surface colonization (larval settlement, bedload transport and swimming), an indirect approach was used. Emergence traps, settlement traps, and bedload traps (Fig. 3) were used to determine the sizes and characteristics of organisms which were collected while actively swimming, settling from the water column, or dispersed during periods of sediment transport. These traps were

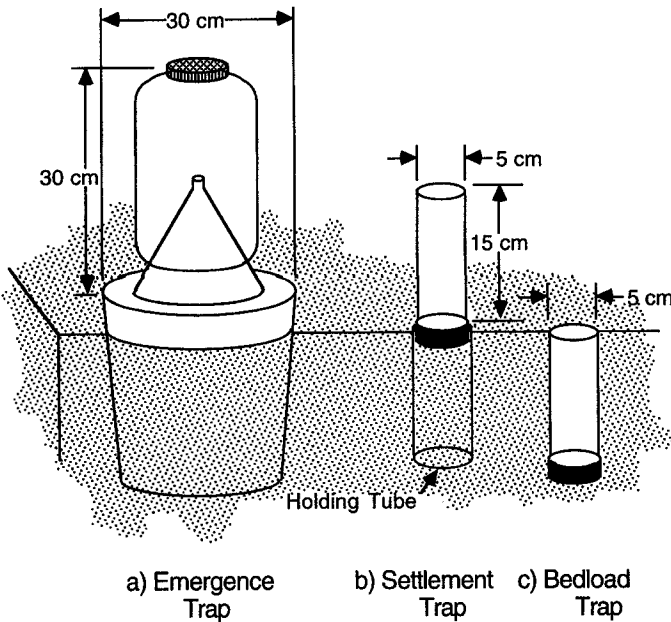


Figure 3. Dispersal Traps. (a) Solid body emergence trap shown inserted in the sediment. (b) Settlement trap raised 15 cm above bottom. (c) Cylindrical bedload trap flush with sediment surface.

deployed and sampled daily around the perimeter of the 9×15 -m experimental disturbance area during the same period of time that the disturbance treatments were deployed.

Each emergence trap (modified from Ambrose, personal communication) was made of a bottomless, plastic gallon jar welded to an inverted 20-cm diameter, plastic funnel which was affixed to the lid of a 5-gallon bottomless bucket (Fig. 3a). The bucket was pressed into the sediment to approximately 2 cm from the top. The mouth of the gallon jar was covered with 300- μ m mesh to allow for water inflow. Organisms emerging from the bed could swim up through the funnel and were captured in the gallon jar. These solid-plastic traps were used because similar plastic traps have been shown to capture polychaetes emerging from the sediment with higher efficiency than other trap designs (Youngbluth, 1982). Also, the solid plastic bucket prevented organisms resuspended outside the emergence trap from entering the gallon jar so that only actively swimming organisms were collected. The traps were sampled daily by washing the contents into a 63- or 125- μ m screen with a squirt bottle and were redeployed in a new location along the perimeter of the 9×15 -m area, not in line with the current direction. The contents were preserved in 10% buffered formalin. Later, the contents were washed over a 125- μ m screen, transferred into 70% ethanol, and sorted under a dissecting microscope.

Settlement traps were made of butyrate plastic tubing with a 5-cm inner diameter (I.D.), a 5.6-cm outer diameter (O.D.), and 15-cm height. The bottom of the tubing was covered by a plastic cap. The traps were inserted into the mouths of butyrate holding tubes (6-cm

I.D.) which were imbedded in the sediment so that the bottom of the traps were secured to the sediment surface while the tops were 15 cm above the bed (Fig. 3b). These traps were sampled daily in the same manner as the emergence traps and returned to the same holding tubes. The trapping efficiency of traps of similar design and aspect ratio in 10 cm sec.⁻¹ flume flow has been shown to be approximately 60% for particles with an average Stokes theoretical settling velocity of 0.015 cm sec.⁻¹, close to that of small larvae (Butman, 1986; 1989).

Bedload traps were identical to settlement traps, however, they were buried so that the opening was flush with the surface of the sediment. This was accomplished by coring with a 6-cm I.D. core and then rapidly inserting the 5.6-cm O.D. bedload trap into the hole. The efficiency of this type of trap is close to 100% if the diameter is greater than 100 times the diameter of the sediment being collected (Hubbel, 1969). Because 71% of the sediment at the study site fit this criterion, it is likely that the efficiency of sediment collection is high, although it may be less than 100%. Field tests by Emerson (1991) suggest that bedload traps of similar design provide a reasonable assessment of changes in bedload transport rate. The contents of the bedload traps were collected and preserved daily. When more than 100 ml of sediment were collected, the samples were split with a plankton splitter and organisms from a subsample were sorted and enumerated. The traps were replaced in a new location around the perimeter of the experimental area after each sampling.

Because the three types of traps potentially collected with different efficiencies, the number of organisms collected by each trap design could not be compared quantitatively. Instead, the traps were used to qualitatively describe organism dispersal. If a species (or a particular life-history stage of that species) was collected in emergence traps, it was concluded that at least some individuals of that species were swimming at the time the trap was deployed. If organisms in the size range of newly settled juveniles were collected in settlement traps, then larval settlement was occurring. If a species, or a life-history stage of a species, was collected in bedload traps but was not collected in settlement or emergence traps, it was concluded that individuals of that species were dispersed by bedload transport.

Sizes of colonizing taxa possessing a planktonic larval stage (*Polydora cornuta* and *Capitella* spp., Table 1) were measured in the laboratory to determine the proportion of colonization which could be accounted for by larval settlement. Sizes of *Polydora cornuta* were determined by counting the number of setigers under a dissecting microscope. Setiger number for fragmented animals was estimated by measuring the width of the fifth setiger (W , in mm) which is related to setiger number (S) by the relationship: $S = 8.42 + 52.44(W)$, $R^2 = 0.88$ (Zajac, 1991). For *Capitella* spp., the width of the widest part of the thorax was measured with an ocular micrometer.

Because sediment transport primarily moves surface sediment, the effect of this process on colonization will in part depend upon the vertical distribution of organisms within the sediment. Composition and vertical distribution within the sediment of the ambient community was determined by sampling fauna from haphazardly chosen locations at the site (not within defaunated patches) with 5-cm diameter cores ($n = 3$) taken the day after

Table 1. Relevant life-history traits for the dominant polychaete species at the study site in the Poquonock River Estuary.

Species	Family	Developmental mode	Mobility	Reference
<i>Streptosyllis arenae</i>	Syllidae	Direct, brooded on underside of female	Motile	Personal observation
<i>Parapionosyllis longicirrata</i>	Syllidae	Direct, brooded on underside of female ^a	Motile	Pettibone, 1963
<i>Brania wellfleetensis</i>	Syllidae	Direct, brooded on underside of female	Motile	Pettibone, 1963
<i>Pygospio elegans</i>	Spionidae	Planktonic, ^b direct or asexual	Tube dweller	Rasmussen, 1953
<i>Polydora cornuta</i>	Spionidae	Planktonic, ^b brooded	Tube dweller	Thorson, 1946
<i>Capitella</i> spp.	Capitellidae	Planktonic, ^c brooded	Tube dweller	Grassle and Grassle, 1976
<i>Nereis (Neanthes) acuminata</i>	Nereididae	Direct, brooded in tube ^d	Tube dweller, Motile	Pettibone, 1963

^aBrooded larvae were found in May and June but none were found in September.

^bPlanktonic development was never observed at the Poquonock River study site although asexual reproduction occurred.

^cDuration in plankton is 12–24 days (Anger *et al.*, 1986). Peak in reproduction occurs in mid-June (Zajac, 1991).

^dDuration in plankton is minutes to weeks depending upon the species (Grassle and Grassle, 1976).

^eLarvae are brooded in tube for approximately 21 days and possess 18–20 setigers upon release (Pesch *et al.*, 1987).

the disturbances were deployed and on each subsequent sampling date. To determine the vertical distribution of infauna, cores were sectioned in the lab with a fine-scale extruder (Fuller and Butman, 1989) at 0-0.5-, 0.5-1-, 1-2-, 2-4-, 4-6-, and 6-10-cm intervals. These cores were preserved and sorted in the same manner as cores from the disturbance treatments.

c. September colonization experiment

To determine the relative importance of the four colonization mechanisms at a time when infaunal reproduction rates were low, the June colonization experiment was repeated from September 5 to September 25, 1990. The September experiment was identical to the June experiment except for the time of year and for slight changes to the settlement and bedload trap designs and improvement of the TST. The 150- μ m mesh on the TST treatments was successfully secured to the plastic holding ring with cyanoacrylate (super-glue).

Changes in dispersal trap designs, which corrected minor problems experienced in the June experiment, included a 28-cm diameter cement collar added to the top of the 5.8 cm (I.D.) butyrate holding tube that secured the settlement traps to the sediment. This collar was flush with the bed, reduced erosion around the holding tube and held the bottom of the

trap more securely to the sediment surface, lessening the chance of the trap being washed away by the current. The bedload traps were modified so that longer tubing could be used. The bedload traps in the June experiment were often filled completely with sediment after 24 hours so that the total amount of sediment transported could not be accurately measured. In order to implant longer traps in the sediment, a PVC outer sleeve was built which could be inserted into a hole carefully excavated in the sediment. The trap fit snugly into the sleeve so that no material was lost between the trap and the sleeve and it could easily be removed for sampling (after Emerson, 1991). The bedload traps were 46 cm in length for the September experiment, and they were deployed 48 hours before sampling to allow disturbance of the sediment surface associated with implantation to be obliterated. The traps were then sampled and returned to the PVC sleeve daily.

d. Sediment transport experiment

If organisms colonize defaunated patches by bedload transport, it follows that colonization rate might be a function of sediment transport rate. The effect of sediment transport on infaunal colonization rates at the study site was assessed by deploying NST disturbances and bedload traps on three dates associated with spring, neap and mid tides. Observations of sediment transport at the site suggested that deployment of experimental disturbances during these time periods would expose them to a range of sediment transport rates. Four replicates of the NST were deployed on July 6 (spring tide), 12 (neap tide), and 17 (mid tide), 1991. The disturbances were inserted at each corner of an array with 1.5 m sides which was arranged so that the replicates were not in line with one another relative to the direction of current flow. Each defaunated patch was sampled after 2 days with a 6-cm I.D. core and the top 4 cm were preserved and sorted. At the same time, 3 bedload traps with PVC sleeves (as in the September colonization experiment) were deployed at the site, adjacent to the NST disturbances. The volume of sediment in each trap was measured and the trap contents were emptied daily.

e. Growth rates of *Capitella* spp.

Growth rates of newly settled *Capitella* spp. at the study site were measured in the laboratory. These measurements were necessary in order to estimate the number of *Capitella* which colonized the disturbances via larval settlement based on colonist size. As it was not clear which species of *Capitella* occurred at the site, growth rate data from the literature could not be used. On May 29, 1992, 10 settlement traps (same design as used in the June experiment) containing 2-3 ml of freeze-thawed sediment were deployed at the study site for 24 hours to collect newly settled *Capitella*. Seven of the traps were recovered. The contents of three of the traps were immediately preserved upon collection while the contents of the other four were sieved over a 63- μ m screen and placed into a 350-ml finger bowl containing freeze-thawed sediment from the study site. The finger bowl was placed into a 32.5 liter aquarium filled with 5- μ m filtered seawater. Cultured organisms were

preserved five days later. Water temperature in the aquarium averaged 17°C over the five day period. Sizes of animals recovered were measured as discussed previously.

f. Statistical analysis

Two-sample comparisons between numbers of organisms for each species were analyzed by *t*-tests after testing for homoscedasticity by the *F*-max test. If a $\log_{10}(x + 1)$ transformation of the data did not homogenize variances, an approximate *t*-test was used (Sokal and Rohlf, 1981). The $\log_{10}(x + 1)$ transformation was also used to normalize distributions if it improved the goodness of fit to the normal distribution of the least normal treatment in a comparison, based on the Kolmogorov-Smirnov D-max statistic. When comparing infaunal densities in the NST and SST disturbances from the June experiment, the one-tailed hypothesis of reduced abundance in the SST relative to the NST was tested. For comparisons of more than two treatments, fixed-effects analysis of variance was used.

The heterogeneity chi-square statistic (total chi-square minus pooled chi-square) was calculated to determine if habitat partitioning by depth occurred at the study site. A heterogeneity chi-square value exceeding its degrees of freedom indicated segregation of species into different depth intervals (see Jumars, 1975, for an application of this statistic to infaunal spatial patterns). Differences in depth-distributions among species were graphically displayed using correspondence analysis by the methods of Greenacre (1986). Correspondence analysis is a geometric representation of the calculated chi-square statistic (Greenacre, 1984).

Tests of correlations were made using Kendall's rank correlation method (Kendall, 1962). Differences among size-frequency distributions were tested using the Kolmogorov-Smirnov two-sample test (Sokal and Rohlf, 1981). Whenever a hypothesis was tested more than once with the same statistical test in a given experiment, results were corrected for Bonferroni's inequality by dividing the alpha level by the number of tests conducted (Miller, 1966). Results of statistical tests which were significant prior to the Bonferroni correction, but not afterward, are also presented. Statistics were computed using StatView SE + Graphics and SAS (1985) software or by hand using the methods outlined in Sokal and Rohlf (1981). The alpha level chosen for tests of significance was 0.05.

3. Results

a. General description of the community

The community studied was primarily composed of fourteen species of polychaetes which accounted for over 80% of individuals at the study site (Shull, 1992). Seven species constituted 96.8% of the total number of polychaete colonists during the May pilot study. Pertinent life history characteristics of these seven species are summarized in Table 1. This study focused solely on colonization dynamics of polychaetes because they were the dominant taxon at the site and opportunistic polychaetes are typically rapid colonizers of

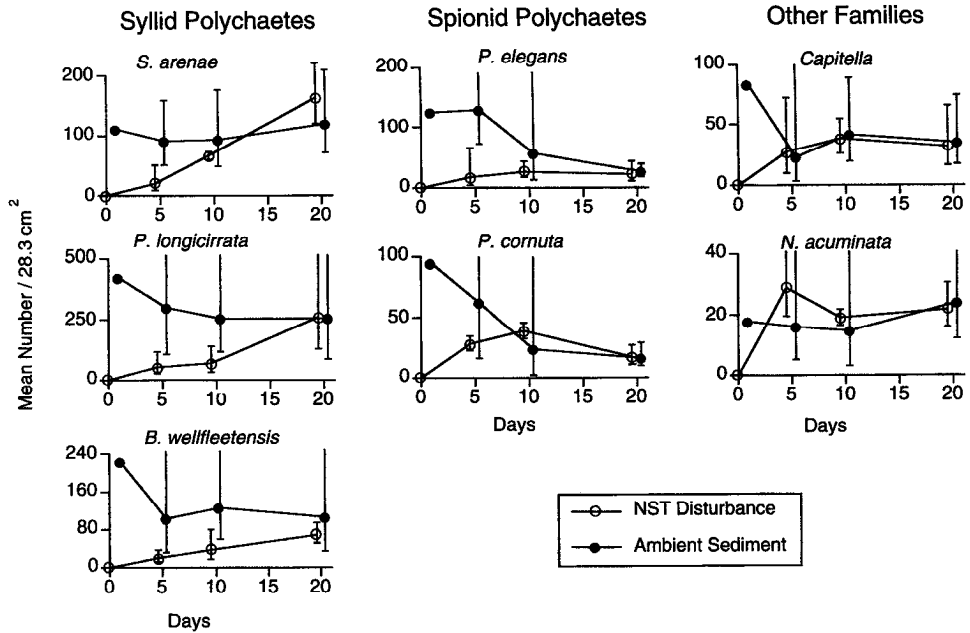


Figure 4. Numbers of individuals recolonizing the NST disturbances (open circles) after 5, 10, and 20 days for the seven most common polychaete species. Closed circles represent ambient densities. Circles belonging to the same treatment are connected for clarity. Although ambient and NST samples on days 5, 10, and 20 were taken on the same date, the circles have been offset to show error bars (95% confidence limits) more clearly. Confidence limits were calculated after a $\log_{10}(x + 1)$ transformation. Back-transformed values are shown. Portions of error bars extending above ordinate axis limits have been omitted.

disturbed areas (e.g., Grassle and Grassle, 1974; McCall, 1977). Taxa which colonized the disturbances in appreciable numbers but were not considered included: oligochaetes, the bivalve *Gemma gemma* and the mud snail *Hydrobia* sp.

b. Patch colonization rates

Response of the numerically dominant polychaete species to small-scale disturbances during the June colonization experiment was rapid (Fig. 4). For the most part, densities in NST disturbances approached ambient densities asymptotically. No species became disproportionately abundant within experimental disturbances. Five days after the creation of the defaunated treatments, densities of two species with planktonic development, *Polydora cornuta* and *Capitella* spp., and densities of *Nereis (Neanthes) acuminata* in NST disturbances had reached ambient densities (Fig. 4). By 10 days, densities of two syllid polychaetes, *Streptosyllis arenae*, *Brania wellfleetensis*, and a tubicolous spionid polychaete, *Pygospio elegans*, in NSTs were not significantly different from ambient densities. By

20 days, densities of all species in the disturbances were the same as in ambient sediment. After reaching ambient densities, changes in abundances in NST disturbances of the most rapidly colonizing species subsequently matched changes in ambient densities (Fig. 4). Changes in ambient densities were not significant for most species during the 20 day experiment. Densities of *P. elegans*, however, decreased significantly from days 5 to 20 (ANOVA, $F_{[2,6]} = 12.04$, $p = 0.008$).

Because densities of most species in the NSTs reached ambient levels within 10 days, organism abundance in defaunated patches after five days most closely approximated initial colonization rates. Therefore, comparisons of colonization rates among disturbance treatments (NST, SST, TST) were made at the five-day deployment period. Making comparisons at this time should also minimize the complicating effects of post-colonization processes (such as competition, predation, food limitation or within-patch reproduction by brooders) in determining colonist densities.

c. Colonization treatments

Data from colonization treatments were used to determine if colonization was primarily by burrowing or from the sediment surface. The mean number of the syllid polychaete, *Parapionosyllis longicirrata*, colonizing the SST treatment in June after five days was significantly lower than the number colonizing the NST control (Fig. 5; one-tailed *t*-test, $t = 3.3$, $p = 0.0066$). Abundances in the SST were less than 30% of abundances in the NST. This suggested that burrowing was the primary colonization mechanism for *P. longicirrata* in June. For the other six species, there were no significant differences in densities between the NST and SST treatments (Fig. 5).

During September, a significant treatment effect was found for *S. arenae* by ANOVA (Fig. 6, $F_{[2,12]} = 8.74$, $p = 0.005$). The number of *S. arenae* was significantly lower in the TST treatment than in the NST and SST treatments (Scheffè *F*-test multiple comparison method, Fig. 6). Densities in the TST were less than 37% of NST densities. This suggested that *S. arenae* colonized mainly from the sediment surface. Because the spionids, *P. elegans* and *P. cornuta*, did not colonize in high numbers (no *P. elegans* and only two *P. cornuta*) in September, comparisons between the NST and TST were not made. For *B. wellfleetensis*, *Capitella* and *N. acuminata*, there were no significant differences in densities among the three treatments. As in the June experiment, the mean number of *P. longicirrata* was lower in the SST than in the NST. Although *P. longicirrata* densities in the SST were just 53% of densities in the NST this difference was not statistically significant in September. When differences in numbers of colonists in the NST and SST disturbances for June and September were analyzed using a 2-way ANOVA with colonization treatment and date as main effects, a significant difference among treatments was found for *P. longicirrata* ($F_{[1,15]} = 12.2$, $p = 0.004$). The Bonferroni corrected date by treatment interaction term was not significant ($p = 0.017$). Thus, burrowing was an important colonization mechanism for *P. longicirrata* in June and September. There were no significant differences between NST and SST for the remaining species as determined by 2-way ANOVA.

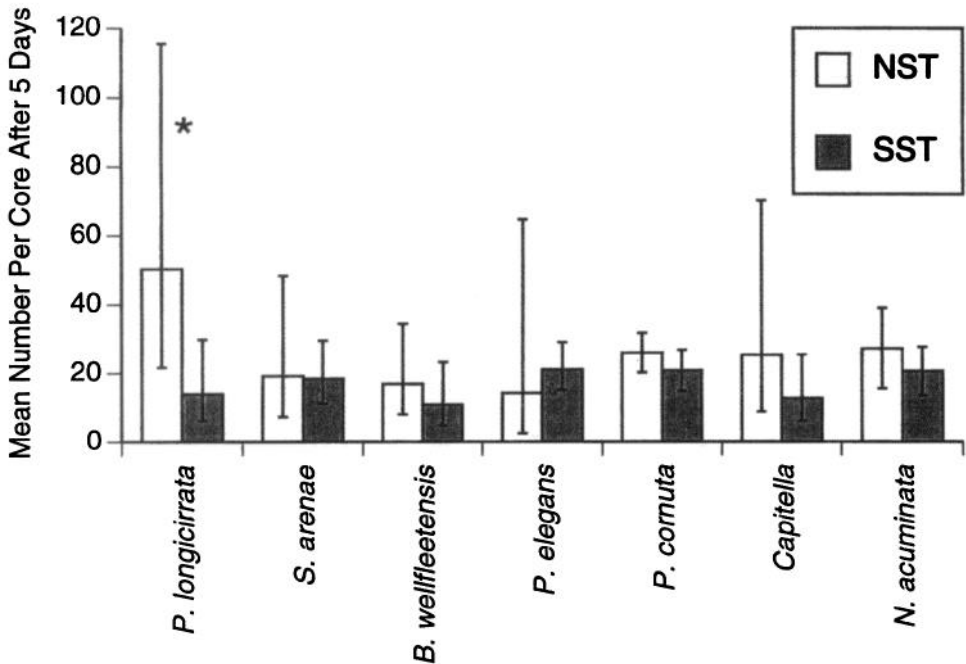


Figure 5. Numbers of individuals of the seven polychaete species colonizing the NST (open bars) and the SST (shaded bars) disturbances during the June colonization experiment. Error bars indicate 95% confidence limits. Mean values and confidence intervals for *S. arenae*, *P. longicirrata*, *B. wellfleetensis*, *P. elegans*, and *Capitella* were calculated after a $\log_{10}(x + 1)$ transformation. Back-transformed values are shown. Asterisks denote significant differences between NST and SST densities as determined by one-tailed *t*-tests ($p < 0.007$, α -value divided by 7 to correct for Bonferroni's inequality).

d. Dispersal traps

Data from dispersal (emergence, settlement and bedload) traps were used to characterize "surface" dispersal mechanisms (other than subsurface burrowing) employed by the colonizing species (Fig. 7). As the number of individuals collected in bedload traps is known to be correlated with the quantity of sediment collected (Commito *et al.*, 1995), this quantity was normalized to the number per 100 ml of sediment so that traps containing different amounts of sediment could be compared.

This analysis was particularly appropriate for *S. arenae* based on the results of the colonization treatments which demonstrated this species colonized primarily from the surface. In June, *S. arenae* (Fig. 7a) was found in all three types of traps although only one individual was found in a settlement trap. All *S. arenae* collected in emergence traps were reproductive adults possessing enlarged bodies and swimming setae while only 4% of *S. arenae* colonizing the disturbances possessed those characteristics. The syllids, *P. longicirrata*, *B. wellfleetensis*, and the spionid, *P. elegans*, were found in bedload traps and a single

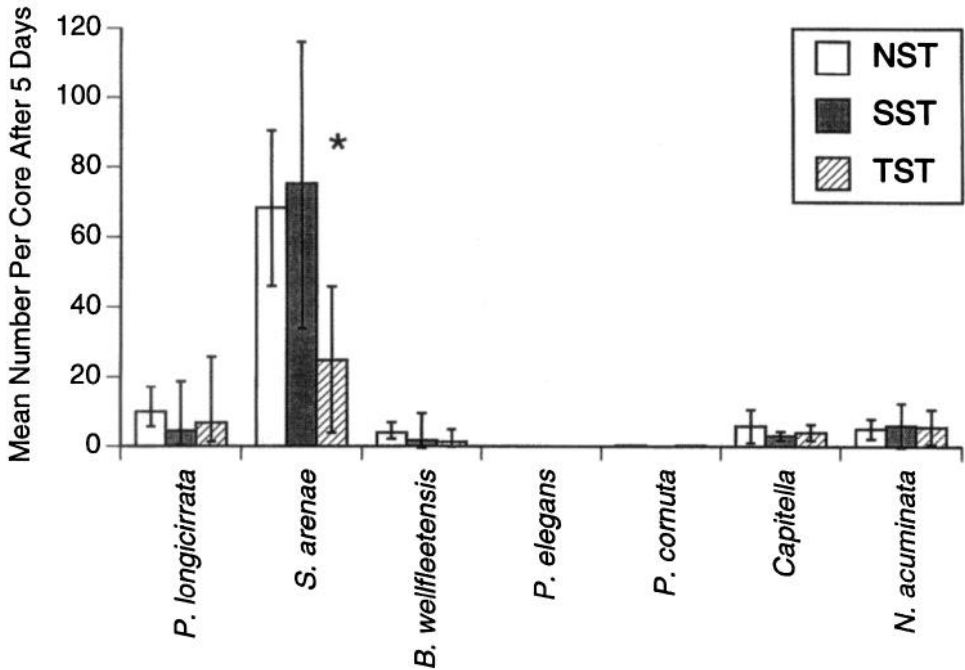


Figure 6. Mean numbers of individuals of the seven most common polychaete species colonizing the NST (open bars), SST (shaded bars) and TST (hatched) disturbances after five days during the September colonization experiment. Error bars indicate 95% confidence limits. Mean values and confidence intervals for *P. longicirrata* and *B. wellfleetensis*, were calculated after a $\log_{10}(x + 1)$ transformation. Back-transformed values are shown. Asterisks denote significant differences between treatments as determined by ANOVA ($p < 0.01$, α -value divided by 5 to correct for Bonferroni's inequality) and Scheffè multiple comparison tests.

P. longicirrata was found in an emergence trap. Two species possessing planktonic larvae, *P. cornuta* and *Capitella*, were found in settlement traps and bedload traps. *P. cornuta* was collected in emergence traps as well. The nereid polychaete, *N. acuminata*, was found in all three types of dispersal traps. Individuals of all species collected in emergence traps were post-larval forms except for *P. cornuta* which were larvae (less than 15 setigers in length).

During the five day deployment in September (Fig. 7b), *P. longicirrata* and *S. arenae* were not found in emergence traps but were collected in bedload traps and one individual of each species was found in a settlement trap. *B. wellfleetensis* and *N. acuminata* were caught only in bedload traps. *Capitella* was found in bedload traps and in settlement traps while *P. cornuta* was found in all three traps. *P. cornuta* was the only species found in emergence traps in September and all individuals collected possessed approximately three setigers suggesting that these larvae were captured as they left the bottom to begin the planktonic phase of their life-cycle.

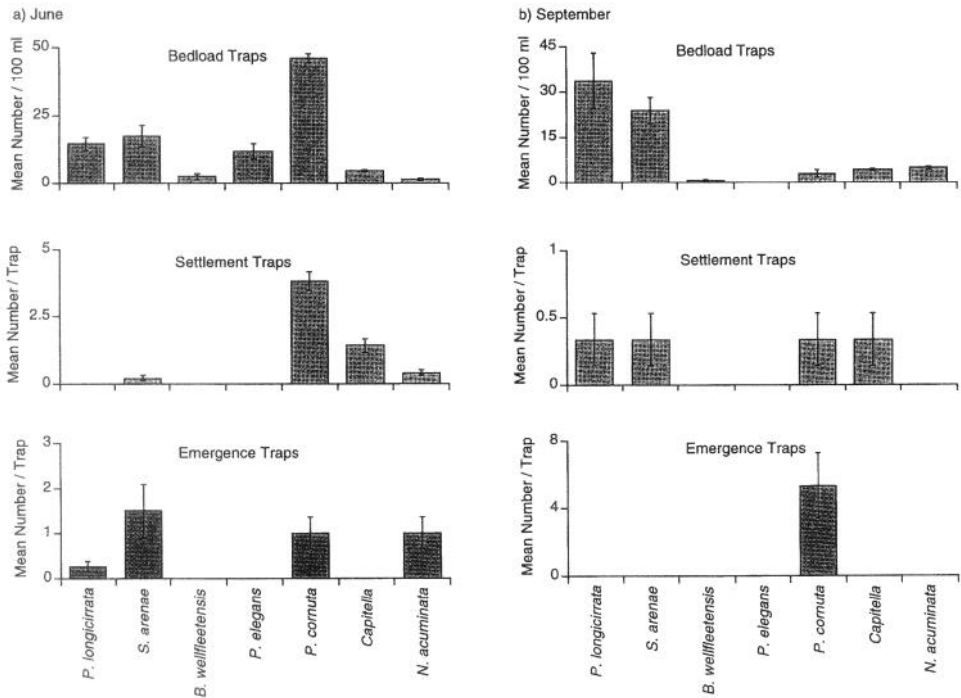


Figure 7. Mean numbers (± 1 S.E.) of organisms captured in the bedload traps (individuals per 100 ml sediment, $n = 3$), settlement traps (individuals per trap, $n = 5$) and emergence traps (individuals per trap, $n = 4$) during June (a) and September (b).

e. Size distributions

P. cornuta and *Capitella* produced planktonic larvae during the experimental periods. Size distributions of these two taxa were examined to determine the relative importance of larval settlement versus colonization by post-larvae. Size distributions of individuals of these taxa collected in settlement and bedload traps and NSTs are shown in Figure 8.

P. cornuta collected in the settlement traps (Fig. 8a) averaged 13 setigers in length. Because *P. cornuta* tends to settle at 15 setigers (Blake, 1969) and could potentially grow one or two setigers before the trap was sampled (Rice, 1975), 12 to 17 setigers was considered to be the size range of newly settled (within 24 hours) *P. cornuta*. This is the same size range of *P. cornuta* that Levin (1984) found settling into cartons placed on the sediment surface for 24 hours.

P. cornuta found in bedload traps (Fig. 8a) averaged 18 setigers ± 3.4 (s.d.) in length. Individuals within the size range of newly settled post-larvae, 12 to 17 setigers, made up 50.5% of the total number captured in bedload traps. The rest were larger than this size range. Differences between bedload trap and settlement trap size-frequency distributions

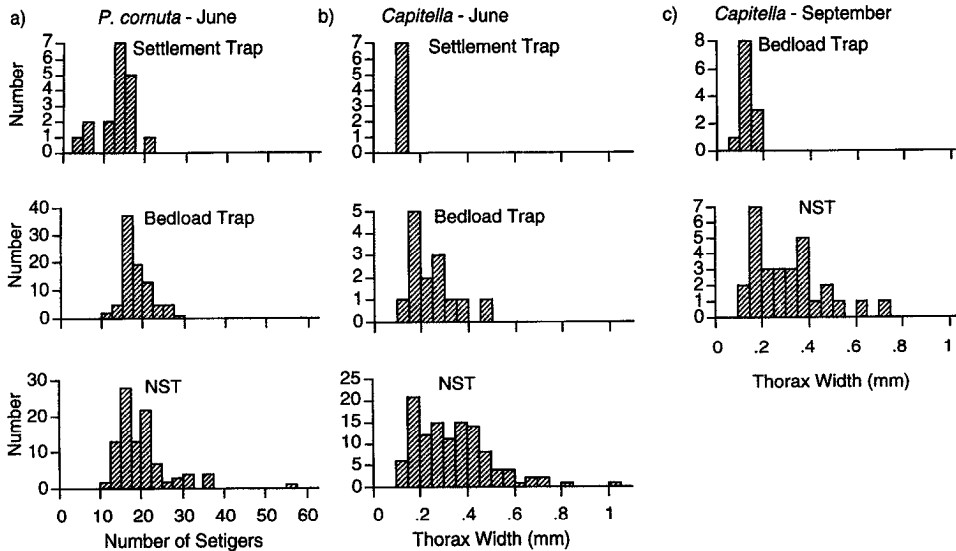


Figure 8. Size-frequency distributions of *P. cornuta* (a) and *Capitella* (b) in settlement traps, bedload traps, and NST disturbances sampled after 5 days during the June colonization experiment. *Capitella* spp. size-frequency distributions in bedload traps and NST disturbances during September are shown in (c).

were found to be marginally significant (Kolmogorov-Smirnov two-sample test, $p = 0.024$ compared to the Bonferroni-corrected $\alpha = 0.017$).

Within the NST, *P. cornuta* averaged 19.9 ± 6.6 (1 s.d.) setigers (Fig. 8a). Forty-three percent of the colonists were within the size range of newly settled individuals (<17 setigers in length) while 79% were within the size range of individuals that potentially colonized via larval settlement during the five-day deployment period given a growth rate of 1 setiger per day (less than 23 setigers; Rice, 1975). The size-frequency distribution of *P. cornuta* within the NST was not significantly different than the size-frequency distribution in bedload traps ($K-S$ test, $p = 0.28$), and was marginally different from the settlement trap size-frequency distribution ($K-S$ test, $p = 0.026$).

The average thorax width of settling *Capitella* was $120 \mu\text{m} \pm 11 \mu\text{m}$ (s.d.). Individuals between 105- and 140- μm in width were considered to be in the size range of newly settled *Capitella* (Fig. 8b). *Capitella* thorax widths (Fig. 8b) measured $240 \mu\text{m} \pm 101$ (s.d.) in the bedload traps. All but one of the individuals in the bedload traps (93%) were larger than the size range of newly settled *Capitella*. The average thorax width of *Capitella* colonists in the NST after 5 days was $339 \pm 162 \mu\text{m}$ (Fig. 8b). Five percent of the *Capitella* were within the size range of newly settled individuals ($\leq 140 \mu\text{m}$ thorax width) while 33% were within the size range of individuals which potentially settled as larvae given the maximum measured laboratory growth rate of 14- μm (thorax width) per day ($\leq 234 \mu\text{m}$). The size-frequency distribution of *Capitella* in the NST was significantly different than the

size-frequency distribution in the settlement traps (K - S test, $p = 0.015$), but not significantly different from the size-frequency distribution of *Capitella* collected in the bedload traps (K - S test, $p = 0.25$) or collected in settlement traps and cultured for five days (K - S test, $p = 0.068$).

Because few *P. cornuta* colonized during September, size frequencies were measured for *Capitella* only (Fig. 8c). The single *Capitella* caught in a settlement trap had a thorax width of 117 μm . Seven percent of the *Capitella* within the NST disturbances were within the size range of newly settled individuals ($\leq 140 \mu\text{m}$ thorax width) while 41% were in the same size range as individuals potentially settled into the patch as larvae ($\leq 234 \mu\text{m}$).

f. Vertical distributions

It is likely that the depth distributions of organisms will affect their susceptibility to entrainment and bedload transport. Although all species were concentrated within the top 4 cm of the sediment, species at the site were segregated in different depth intervals within the top 4 cm throughout the study period (Fig. 9, May: heterogeneity chi-square (hc - s) = 4.9, $p = 0.04$; June: hc - s = 3.59, $p = 0.01$; September: hc - s = 3.57, $p = 0.01$). Although abundances of most species were highest in the top 1 cm, abundances of two syllid polychaetes, *P. longicirrata* and *B. wellfleetensis*, were more closely associated with the 2- to 4-cm depth interval throughout the summer (Fig. 9). The abundance of *N. acuminata* was also highest in the 2-4 cm depth interval in June.

g. Sediment transport experiment

To examine if sediment transport rate affected colonization rate, the number of individuals colonizing the NST disturbances after two days were plotted against the average volume of sediment accumulated in the traps each day during each two day deployment period of the sediment transport experiment (Fig. 10). Only those species which averaged more than two individuals in a core during the sampling periods were included in the analysis. The number of *S. arenae* colonizing was positively correlated with the average volume of sediment collected (Fig. 10). The number of *P. longicirrata*, *B. wellfleetensis*, *N. acuminata* and *Capitella* found in the disturbances was not related to the volume of sediment collected although, for *Capitella*, the trend suggested a (marginally significant, $p = 0.0132$ compared to the Bonferroni corrected $\alpha = 0.01$) negative correlation (Fig. 10).

4. Discussion

a. Colonization mechanisms

Past research on macrofaunal colonization mechanisms has primarily focused on pair-wise comparisons of certain colonization modes such as adult versus larval recruitment (e.g., Santos and Simon, 1980), larval recruitment versus horizontal migration (e.g., Smith and Brumsickle, 1989), and active versus passive recruitment (e.g., Savidge and

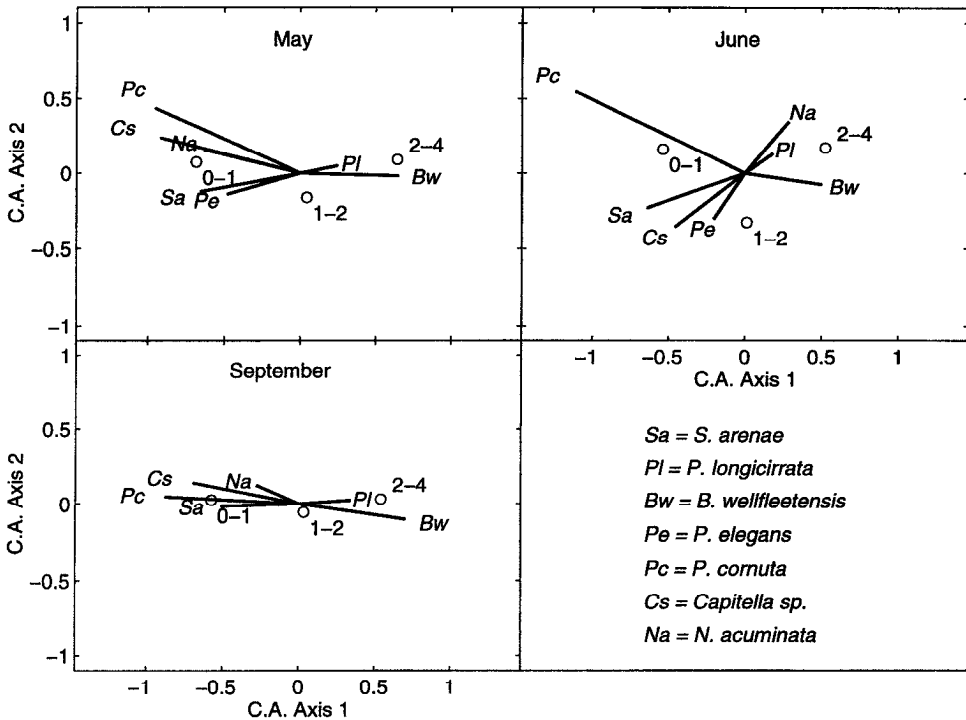


Figure 9. Two-dimensional display of depth-distribution data by correspondence analysis. 100% of variation in species depth distributions were summarized by the first two axes displayed. Each vector represents a species. Circles indicate the location of 0- to 1-cm, 1- to 2-cm and 2- to 4-cm depth intervals in two-dimensional space. An acute angle between a species vector and another species vector, or a line connecting a depth location and the origin, indicates a positive association. Angles between vectors (or between a vector and a line connecting a depth location with the origin) of greater than 90 degrees indicate negative association.

Taghon, 1988). The purpose of this research was to compare the relative importance of all colonization mechanisms that could have potentially occurred at the study site: larval settlement, burrowing, bedload transport, and swimming. The relative importance of these colonization mechanisms could be determined by reasoning from size distributions of colonists, numbers of colonists found in colonization treatments, and collections from dispersal traps. Information on colonization mechanisms was then used to formulate hypotheses on how colonization rates should change as a function of sediment transport rate. These hypotheses were tested by measuring colonization rates during periods with different sediment transport rates.

Species possessed more than one colonization mechanism. For a few species, it was possible to determine the primary colonization mechanism. Important colonization modes found in this study are summarized in Table 2. The reasoning behind the assignment of specific colonization mechanisms in this table will be described next.

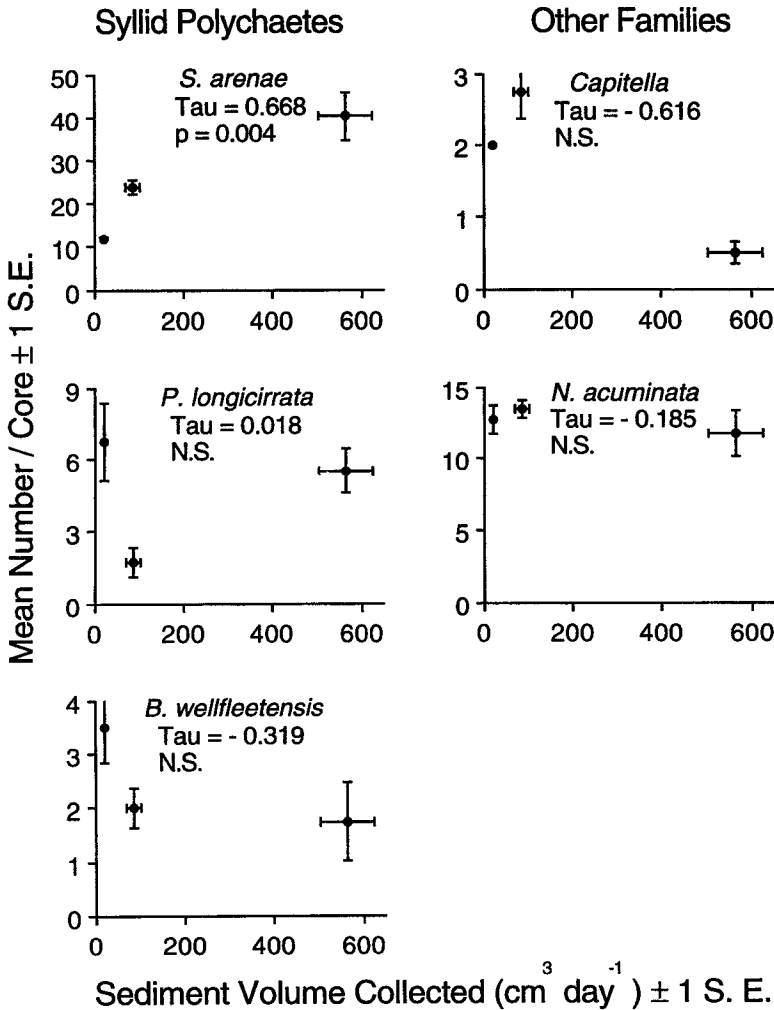


Figure 10. Mean number of individuals of five polychaete species that colonized NST disturbances after two days during the sediment transport experiment are plotted against the average volume of sediment collected in the bedload traps during the 2 day deployment period. Vertical and horizontal error bars indicate the standard error of the mean. N.S. = no significant correlation ($p > 0.01$, α -value divided by 5 to correct for Bonferroni's inequality).

i. Larval settlement. Size ranges of species with a planktonic larval stage indicated the proportion of colonization which could be attributed to larval settlement. *P. cornuta* and *Capitella* were the only species at the study site which possessed a planktonic larval stage and could have potentially colonized by larval settlement. The size range of *P. cornuta* found in NST disturbances suggested that larval settlement was the primary colonization mechanism for this species, accounting for between 43% and 79% of colonization.

Table 2. Summary of polychaete colonization mechanisms (***) = the most important mechanism, * = mechanisms used to a lesser degree, ? = insufficient data). Note: Post-larval swimming was a colonization mechanism in June but not in September. Larval settlement also appeared to be more important in June than in September.

Species	Larval settlement	Burrowing	Bedload transport	Post-larval swimming
<i>Streptosyllis arenae</i>			***	*
<i>Parapionosyllis longicirrata</i>		***	*	*
<i>Brania wellfleetensis</i>		*	*	
<i>Capitella</i> spp.	*	*	*	
<i>Pygospio elegans</i>		?	*	
<i>Polydora cornuta</i>	***	?	*	
<i>Nereis acuminata</i>		*	*	*

However, approximately half the *P. cornuta* collected in bedload traps were 1 to 10 setigers larger than newly settled individuals. This suggests that small, recently settled (less than ten days old) *P. cornuta* were susceptible to entrainment and dispersal during periods of sediment transport. In September, only one individual of *P. cornuta* was collected in a settlement trap and only one colonized NST disturbances. Since larval production for this species peaks in mid-June in this area (Zajac, 1991) it is likely that the low colonization rate in September was due to low availability of planktonic larvae.

In contrast, the size range of *Capitella* colonists suggested larval settlement accounted for just 5% to 33% of colonization in June and between 5% and 40% of colonization in September. Since most *Capitella* colonists were much larger than recently settled post-larvae, larval settlement was not the primary colonization mechanism used by *Capitella*. As burrowing or bedload transport were the only other colonization mechanisms available to *Capitella*, those mechanisms must have accounted for over 60% and possibly as much as 95% of colonization. This conclusion contrasts with results from colonization studies in muddy sediments where *Capitella* spp. was observed to colonize primarily via larval settlement (e.g., Grassle and Grassle, 1974; McCall, 1977). The contrast may be due to differences in size and degree of isolation of experimental disturbances between this and previous studies (Smith and Brumsickle, 1989) or to greater mobility of sediments and organisms in sandy sediments.

A few caveats accompany the results for *Capitella*. First, the importance of larval settlement may have been underestimated because growth rates of *Capitella* cultured in the laboratory at 17°C may have been slower than growth rates of *Capitella* in the field (temperatures varied between 20°C and 23°C). Also, the size distribution of *Capitella* in settlement traps could have been biased toward the larger size classes as settlement traps can be biased toward particles and, potentially, larvae with higher fall velocities (Butman *et al.*, 1986). If *Capitella* recruits grew faster in June than the rate estimated in the laboratory, then a higher percentage of colonists could have potentially colonized via larval settlement in June. However, these potential biases were likely compensated because the maximum

measured growth rate for *Capitella* was used to determine the upper bound for colonization by larval settlement. Second, at the present time, *Capitella* cannot reliably be identified to species after preservation in formalin. Since the species of *Capitella* found at the site were not identified, the exact form and duration of larval development was not known (Grassle and Grassle, 1976). It is thus possible, for example, that individuals captured in dispersal traps may have been different sibling species than those colonizing disturbances. These caveats, however, do not change the conclusions displayed in Table 2. *Capitella* spp. colonized by all mechanisms except swimming.

ii. *Burrowing.* *P. longicirrata* colonized primarily by burrowing from surrounding sediments as demonstrated by significantly lower densities in the SST compared to the NST. Burrowing appeared to be a component of colonization for most of the other species as most were able to colonize the TST disturbance which allowed colonization only by burrowers. Exceptions to this pattern were found for *S. arenae* which colonized mainly from the sediment surface and possibly the spionids, *P. cornuta* and *P. elegans*, which did not colonize in high numbers in September. Studies by Wilson (1981; 1984), however, suggest that *P. elegans* can migrate by burrowing. *Capitella* and *N. acuminata* appeared to colonize by burrowing and from the sediment surface. However, because these two species reached ambient densities sometime before the five day sampling period, the NST patch defaunations may have underestimated colonization rates and increased the probability of finding no differences among treatments for these species.

iii. *Bedload transport.* Organisms captured in bedload traps arrived either by larval settlement, swimming, or were transported along with moving sediment during periods of sediment transport. Because larval settlement and swimming were not occurring in September, organisms collected in bedload traps at this time arrived by bedload transport. Therefore, all species at the site were dispersed to some degree by bedload transport. Individuals collected in bedload traps in June may have arrived by any of the three surface colonization mechanisms. Because colonization for *S. arenae*, which lacks a planktonic larval stage, was primarily from the sediment surface and swimming could account only for 4% of colonization, this species colonized primarily by bedload transport.

In general, the only species collected in settlement traps were those possessing swimming ability or a planktonic larval stage. Since very few individuals lacking these traits were collected in settlement traps, it is likely that during sediment transport, organisms were transported close to the sediment surface rather than in suspension. Thus, the mode of transport of most adult infauna during periods of sediment transport most closely resembled bedload, rather than suspended load, transport.

iv. *Swimming.* Post-larval forms of *S. arenae*, *P. longicirrata* and *N. acuminata* were collected in emergence traps in June which suggested that these species had the ability to swim. Although post-larval swimming was not the primary colonization mechanism for *S.*

arenae which colonized via bedload transport, or *P. longicirrata* which colonized by burrowing, swimming may have been an important component for *N. acuminata*. Because both juvenile and adult *N. acuminata* were collected in emergence traps, organism size or distinct morphological features could not be used to differentiate between individuals which colonized by swimming or by other modes. Therefore, the importance of swimming relative to other mechanisms for *N. acuminata* could not be determined.

In summary, bedload transport appeared to be the most important colonization mechanism for *S. arenae* while larval settlement was most important for *P. cornuta*. *P. longicirrata* colonized primarily by burrowing. Bedload transport and burrowing were mechanisms used by *B. wellfleetensis* and possibly *P. elegans*. *N. acuminata* colonized by swimming (only in June), burrowing and by bedload transport. Finally, *Capitella* colonized by larval settlement, burrowing and bedload transport. In general, larval settlement and post-larval swimming were more important in June than in September. This corresponds to an early summer peak in reproduction for most of these species.

b. Influence of arrival mode on colonization

Knowledge of colonization mechanisms allows one to understand how colonization rates will vary spatially and temporally. For example, if a species colonizes primarily by bedload transport, it follows that colonization rate will likely be correlated with sediment transport rate. During the sediment transport experiment, colonization rate for *S. arenae*, the syllid polychaete which colonized primarily by bedload transport, was positively correlated with the average volume of sediment collected in bedload traps, a measure of relative changes in sediment transport rate (Fig. 10). However, numbers of the other four species which colonized during this experiment were not positively correlated with sediment transport rate. Since these species possessed dispersal mechanisms such as burrowing or swimming in addition to bedload transport, they were able to colonize patch defaunations when sediment transport rates were low. Despite the observation that all species were dispersed to some degree by bedload transport, this mechanism was found to be important for controlling colonization rate only for *S. arenae*.

c. Species characteristics

This study examined colonization mechanisms for a number of representatives from the polychaete families Syllidae and Spionidae. Thus, it was possible to investigate those characteristics which influenced colonization mechanisms among closely related species within these families. In addition, the study examined characteristics of more distantly related polychaetes from the families Capitellidae and Nereididae.

The nereidid polychaete, *N. acuminata*, is an active burrower. It lacks a planktonic larval stage, brooding its young until they reach approximately 18 setigers in length. Therefore, larval settlement was not a colonization mechanism for this species. Instead, burrowing was used. Since swimming is common in nereidids (e.g., Dean, 1978; Goerke, 1984), it was not surprising that swimming was used as a colonization mechanism by this species.

The spionid polychaete *P. cornuta* also broods its young but possesses a planktonic larval stage. The finding that this species colonized primarily via larval settlement is consistent with findings of Levin (1984). This species is tubicolous which could potentially protect large individuals from transport during periods of sediment erosion. However, small, recently settled individuals (<30 setigers) were susceptible to entrainment and post-larval dispersal by bedload transport.

Another spionid, *P. elegans*, though also tubicolous, colonized by dispersal during sediment transport. This species is known to migrate after settlement, probably by burrowing (Wilson, 1981; 1984), although more recent experiments by Wilson (1994) were unable to distinguish burrowing from other colonization mechanisms. It is apparent that the ostensibly sedentary, tubicolous spionids *P. elegans* and *P. cornuta* possessed the ability to relocate themselves as adults and juveniles. This post-larval movement, partly by bedload transport, may have been facilitated by the location of these species within the mobile, top 1-cm layer of the sediment (Fig. 9).

Because the species of *Capitella* at the site was not determined, it was not possible to relate colonization mechanisms to life history characteristics as these vary according to species (Grassle and Grassle, 1976, 1977; Grassle, 1979). However, species in this complex are considered extreme opportunists possessing rapid colonization abilities in many environments (Grassle and Grassle, 1974; Thistle, 1981). The finding that *Capitella* spp. used multiple colonization modes is consistent with the ability of this species to colonize rapidly under many environmental conditions.

Although the three syllid species, *S. arenae*, *P. longicirrata* and *B. wellfleetensis*, are very similar in size, appearance, and developmental mode, they used different colonization mechanisms. Although this result may seem surprising in light of the similarity between these co-familial species, differences in colonization mechanisms may have been due to among-species differences in vertical distribution in the sediment. *S. arenae* was always most abundant near the sediment surface while *B. wellfleetensis* and *P. longicirrata* were more closely associated with the 2- to 4-cm depth interval (Fig. 9). Since sediment transport mobilized the upper 1 cm of sediment of the bed, concentration of *S. arenae* in this layer likely facilitated the entrainment of this species. This is similar to the findings of Grant (1980, 1981a, 1981b) who discovered differences in depth distributions among closely related amphipods which affected colonization ability.

Behavior may also have played a role in bedload transport of *S. arenae*. This species was observed in the laboratory under a microscope to roll up into a ball when dislodged from the sediment in a Petri dish. This reaction was not observed in other species. "Rolling-up" behavior has been related to transport by wave action in another polychaete, *Armandia* sp. (Tamaki, 1987) and may have facilitated bedload transport of *S. arenae*.

Because polychaete species from the same family possess very different colonization mechanisms, making generalizations regarding colonization mechanisms at the family level is problematic. Characteristics which are most important in determining the primary

colonization mechanism include size, mobility, developmental mode and depth distribution. Most of these characteristics can be quite variable within polychaete families.

d. Ecological implications

This study was motivated by the desire to understand the factors influencing early succession of small-scale disturbances in sandflats. Also of interest was examining the question how species lacking a planktonic larval stage, which ostensibly limits dispersal, rapidly colonize disturbances.

The prediction of which species will initially colonize a disturbed sediment patch is critical for predicting the subsequent successional sequence because initial colonists may have demonstrable effects upon later arrivals. In some cases this occurs through inhibition of later arrivals (Whitlatch and Zajac, 1985; Hines *et al.*, 1989), tolerance (Gallagher *et al.*, 1983; Whitlatch and Zajac, 1985) or facilitation (Gallagher *et al.*, 1983; Thrush *et al.*, 1992). Therefore, it is important to understand the processes influencing initial colonization rates.

For species which displayed one primary colonization mechanism, one can predict how colonization rates will vary under different environmental conditions. Other sandflat species with similar characteristics may follow similar patterns. For *S. arenae*, the small surface-dweller, colonization rate was a function of sediment transport rate. For *P. cornuta*, a species possessing planktonic larvae, colonization rate was highest near the peak of larval supply. It is likely that for *P. longicirrata*, a burrower, colonization rate will depend upon the size of the defaunated area (Smith and Brumsickle, 1989). For species which possess more than one colonization mechanism, (i.e., *B. wellfleetensis*, *Capitella*, *N. acuminata*) predicting changes in colonization rate is more difficult.

The results of this study provide an answer to the question how species lacking a larval dispersal stage can be rapid colonizers. Benthic infauna may use a variety of dispersal mechanisms, including more than one mechanism, to colonize recently disturbed sediment patches.

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