
Reproduction and Development of Marine Invertebrates

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23 Dispersal of Soft-Bottom Benthos: Migration through the Water Column or through the Sediment?

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ABSTRACT Experiments were performed in a soft-sediment community in False Bay, San Juan Island, Washington, to examine the route of dispersal of the resident organisms. The dominant organisms were (1) the tube-building spionid polychaetes, *Pygospio elegans* and *Pseudopolydora kempfi*; (2) a guild of burrowing oligochaetes; and (3) epifaunal ostracodes. Azoic patches of sediment of differing size were prepared, and the recolonization of these patches by adult infauna was monitored. Only the central areas of the patches were sampled. The data indicate that colonization rate into the central area of patches is independent of the total size of the patch. Immigration into azoic patches appears to occur largely by vertical migration rather than by lateral migration; that is, the infauna appear to enter the water column and then descend onto the sediment surface rather than to crawl across or within the sediment surface to reach the unoccupied substratum. These data indicate that dispersal of adult infauna, even tube-dwelling ones, may be far more frequent than previously thought.

Introduction

Invertebrates living in soft-sediment communities are frequently classified into functional groups based on motility (Woodin, 1976; Brenchley, 1981). For instance, many infauna such as spionid and maldanid polychaetes build tubes and are considered sedentary organisms. Others, such as bivalves and thalassinid crustaceans maintain burrows in the sediment and are also considered sedentary. Mobile infauna include infaunal burrowers such as opheliid polychaetes and naticid gastropods and mobile epifaunal species such as ostracodes and many amphipods. The assumption is generally made that sedentary species, both those dwelling in tubes and those dwelling in "permanent" burrows, rarely move after settlement. Infaunal mobile species are presumed to migrate exclusively by lateral dispersal through the sediment while epifaunal species either disperse laterally across the surface of the sediment or may disperse vertically by entering the overlying water column and then dispersing laterally. With present information, infauna are generally considered less mobile than epifauna because it is believed that infauna do not undergo vertical migrations and do not often migrate laterally (but see Smith and Brumsickle, 1989).

This model of adult movement is contraindicated by the observation that many presumed sedentary organisms can be found in the plankton. Such organisms include apodous holothurians (Costello, 1946), infaunal bivalves (Dauer et al., 1982), burrow- and tube-dwelling polychaetes (Dean, 1978a,b; Farke and Berghuis, 1979; Dauer et al., 1980, 1982), and many macrofaunal crustaceans (Dauer et al., 1982). In addition, Wilson (1983) showed that tubicolous spionid polychaetes readily relocate in a density-dependent fashion. When densities were artificially

increased, emigration by adults rapidly returned the densities to preexisting levels. Furthermore, areas in which density was artificially lowered were colonized rapidly, converging on ambient density. It was presumed, but not clearly demonstrated, that migration occurs by lateral migration across the surface of the sediment (Wilson, 1983).

In this chapter, I describe a series of experiments designed to determine the rate of colonization of patches of defaunated sediment. Specifically, the experiments were designed to yield insight into the route of immigration: lateral or vertical. I show that the data are consistent with most immigration occurring by animals that are present in the water column which subsequently resettle on the sediment surface.

Materials and Methods

This research was performed in the summer of 1991, in False Bay, San Juan Island, Washington. (For a detailed map of the area, see Pamatmat [1968].) False Bay is a large embayment, approximately 1 km wide and 1 km broad. Most of the water in the bay empties at low tide.

The particular study site used in this study was located in the upper reaches of False Bay at the +1.0-m tide level. The same area was used in previous research (Wilson, 1981, 1983). The sediment in this portion of the bay is a well-sorted fine sand; virtually all of a sediment sample passes through a 250- μm screen.

The infaunal community at this tidal height is characterized by high density but low diversity. Only six taxa are found regularly. The most abundant taxon is a guild of oligochaetes. No attempt was made to identify these to species; instead, all oligochaetes were counted as a single taxon. The other regularly occurring organisms were (1) the spionid polychaetes, *Pygospio elegans* Claparède and *Pseudopolydora kempfi* (Southern); (2) the amphipod crustacean, *Corophium spinicorne* Stimpson; (3) the cumacean crustacean, *Cumella vulgaris* Hart; and (4) a guild of podocopid ostracodes. Both of the spionids maintain vertical tubes which extend to 25 mm below the sediment surface. *Corophium* maintain burrows in the top 50 mm of the sediment. The oligochaetes burrow beneath the sediment surface and do not maintain a "permanent" burrow. The ostracodes scurry across the surface of the sediment. *Cumella* lies buried in the sediment with only its anterior end protruding. Occasionally, however, these cumaceans leave the sediment and swim in the water column, settling down onto the sediment surface at a different location later. Thus, despite the low diversity of organisms in this community, several different functional groups, based on motility, co-occur.

The experimental approach involved creating patches of defaunated sediment in the field and then monitoring recolonization. Sediment was collected from the field in 5-gal buckets and brought to the Friday Harbor Laboratories. All of the supernatant sea water was poured off and replaced with freshwater. The buckets were placed outside the laboratory for at least a week. Prior to commencing an experiment, all of the sediment was sieved to remove any tubes. Visual examination of the sediment indicated that all of the animals had been killed by this procedure.

Matrices of defaunated patches of differing sizes were established as follows. For each matrix, four pairs of wooden dowels were driven into the sediment in a rectangular array of four rows. Each pair of dowels was 3 m apart. Adjacent dowels in either row were 1 m apart. A piece of twine was tautly strung between each pair of dowels. Beginning 75 cm from one dowel, an applicator stick was pushed into the sediment to mark four positions at 50-cm intervals. Each stick marked the center of an experimental area.

Four different cores were used to establish the experimental treatments. The diameters of these cores were: 4.5 cm (designated the A core), 9.5 cm (B core), 16 cm (C core), and 28.5 cm (D

core). Within each row, one of the four cores was centered around the applicator stick and pressed into the sediment. Using a trowel and scoopula, the ambient sediment enclosed in the core was removed to a depth of 50 mm. Azoic sediment, prepared in the laboratory, was then used to replace the sediment within the space defined by the core. After the azoic sediment had been introduced, the core was removed, leaving a patch of defaunated sediment with no barriers to lateral immigration through the sediment. The absence of any type of enclosure insured that no hydrodynamic artifacts would be generated (Hulberg and Oliver, 1980). Each matrix was laid out in a Latin square design (Sokal and Rohlf, 1981).

To ensure that the center of each defaunated area could be precisely relocated, I set up two additional pairs of dowels in the study area; these dowels were within 5 m of the 3-week site. I marked four positions between each pair of dowels at 50-cm intervals as described above and then pushed ten applicator sticks (diameter of 2 mm) into the space surrounded by an A core. After 1 week, I returned to these control dowels and determined again the four experimental positions between each pair of dowels and used the A core to sample each position. The number of applicator sticks sampled was noted. I also sampled the area around the A core to search for any applicator sticks that were not recovered when the position was relocated.

Three experimental matrices were used in this study. The first was erected on 30 June, the second on 7 July, and the third on 14 July 1991. All of the matrices were sampled on 21 July, thus providing colonization data after 1, 2, and 3 weeks. Each defaunated area was sampled with a series of concentric cores. For example, a D-core-sized defaunated area was sampled by first removing the center with the A core, then the B core, then the C core; finally all of the sediment remaining was collected as the D core. For A cores, only the A core was used since none of the sediment outside of it had been defaunated. This procedure permits the comparison of equal areas of defaunated areas which differ in the amount of buffer of defaunated sediment surrounding them. If colonization occurs by lateral movements of infauna, one would expect that the A cores from the A-core-sized areas would have more immigrants than the A cores nested within the B, C, and D cores. However, if colonization occurs via the water column, by waterborne adults, then one would expect no difference in the number in each A core, regardless of the amount of defaunated buffer around it. At the time of sampling of the matrices, five cores (0.008 m²) were taken of the ambient community to establish the natural densities within each matrix. All of the samples were returned to the Friday Harbor Laboratories where each was sieved independently through a 500- μ m screen. Approximately half of the samples were sieved on 21 July. The remainder were kept in buckets which were placed in sea water tables (water temperature of 10°C) to keep the samples cool. These samples were sieved on the morning of 22 July. The relatively coarse screen was chosen so that recently settled larvae would pass through. The explicit purpose of this experiment was to examine colonization of defaunated sediment by adult or juvenile infauna.

The samples were preserved in 5 percent formalin in sea water. Sorting of the samples was done with a Wild stereomicroscope at 12 \times magnification. Only heads and whole organisms were counted.

Statistical analyses were performed on both the A cores and the B cores for each of the three experiments. The C cores (only two replicates per treatment for each matrix) and the D cores (only one replicate per treatment for each matrix) were not analyzed because of insufficient replication. Using a one-way analysis of variance (ANOVA) model, the numbers of each of the six common taxa were analyzed for the A cores as a function of the size of the total defaunated area. The B cores were analyzed with a one-way ANOVA in similar fashion. Scheffé post hoc comparisons

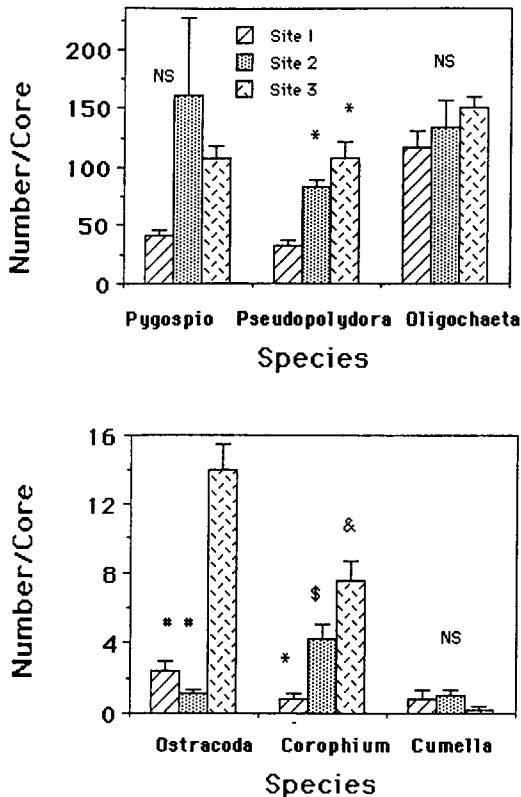


FIGURE 23.1. Comparison of natural densities of the six most common taxa at the three experimental sites. Site 1 is the site of the 1-week experiment, Site 2 the 2-week experiment, and Site 3 the 3-week experiment. Means which share the same symbol are not statistically different ($p > .05$). NS means that there is no statistical difference among any of the three means.

were calculated for each taxon. All of the statistical analyses were done on a Macintosh SE30 using SuperAnova, Version 1.1 (Abacus Concepts).

For both the A and B cores, two-way analyses of variance were performed, testing the effect of position (the size of the total defaunated area) and duration (1, 2, or 3 weeks). In all cases, the interactive term was found to be insignificant. The analyses were then recalculated, removing the interaction term. Comparisons of the average number of immigrants for each taxon were made between the 1-, 2-, and 3-week experiments with Scheffé contrasts.

Results

Figure 23.1 presents a comparison of the ambient densities of the six common taxa at the three experimental sites. Although the three sites were located within 8 m of each other, significant differences in abundance emerged for some taxa. *Pseudopolydora* was more abundant at the Week 2 and Week 3 sites relative to the Week 1 site. Ostracodes were significantly more abundant in the Week 3 site. *Corophium* abundance was significantly least at the Week 1 site, intermediate at the Week 2 site, and greatest at the Week 3 site. *Pygospio*, oligochaetes, and *Cumella* means did not differ among experimental sites.

The results of the control experiment with applicator sticks demonstrated that experimental areas could be precisely located. Of the four groups of ten applicator sticks emplaced in A cores on 14 July, I recovered nine, eight, nine, and ten of the applicator sticks on 21 July. The sticks that

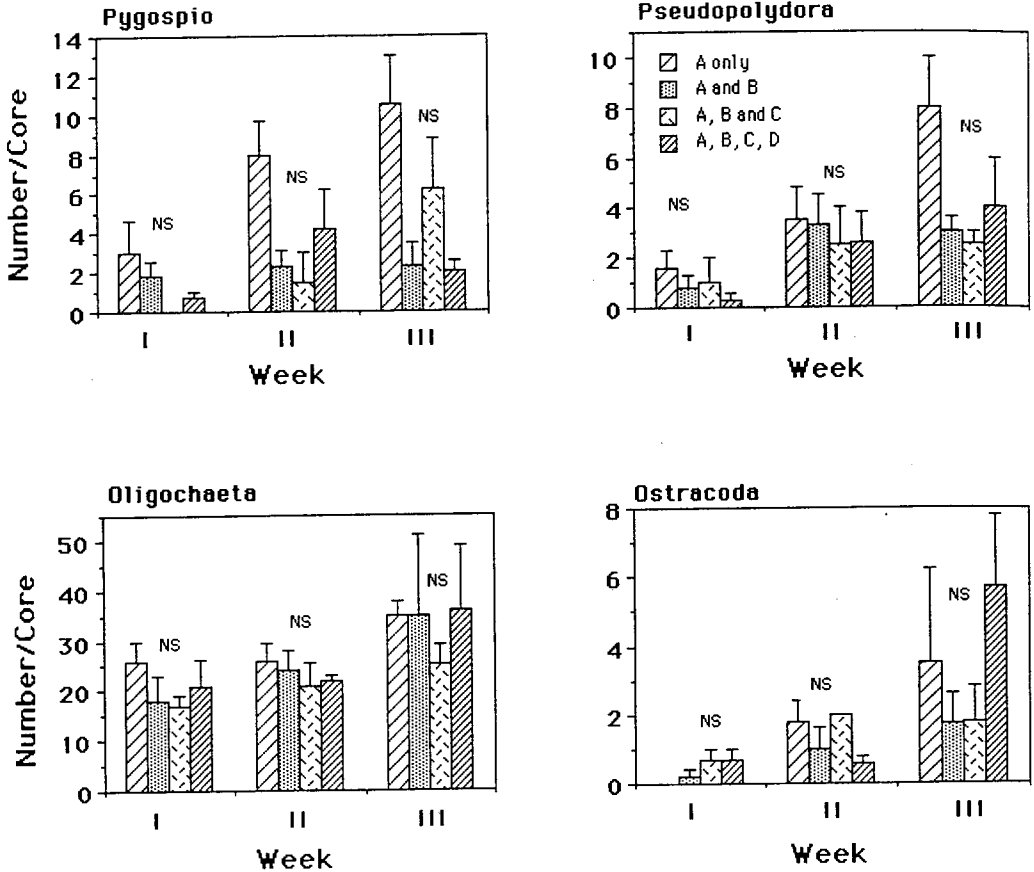


FIGURE 23.2. Results of analysis of the inner (A cores) areas for the four most common taxa in the 1-, 2-, and 3-week experiments. NS means that there is no statistical difference among any of the three means ($p > .05$).

were missed were found to be at the most 4 mm from the outer edge of the A-sized corer. Thus, these data show that I could precisely relocate experimental areas.

Figure 23.2 presents the data for colonization of the central areas, the A cores, for the four most common taxa in the three experiments. *Pygospio* abundance did not differ among the treatments; *Pygospio* density was no greater when the A core was surrounded by the natural community compared to treatments where the A core was encircled by areas of defaunated sediment of three different sizes. These data suggest that colonization of the A cores by *Pygospio* occurred by adults, swept into the water column, which resettled elsewhere. Similar results were found for *Pseudopolydora*, oligochaetes, and ostracodes; the number of these taxa colonizing the A core treatment only were not significantly greater than the remaining treatments with larger areas. Both *Corophium* and *Cumella* showed low abundance in the experimental areas, largely as a function of their relative rarity in the community; the analyses of their experimental abundances will not be presented although they agreed with results for the other taxa.

Figure 23.3 presents the data comparing the abundances of adult colonists among the three different B areas. The A core had been removed from each of these B areas in sampling. There are therefore three treatments, the B ring surrounded by unmanipulated sediment, the B ring surrounded by the C ring, and the B ring surrounded by a C and D ring. For the Week 1 experiment, there were significantly more *Pygospio* in the B only treatment compared to the other two

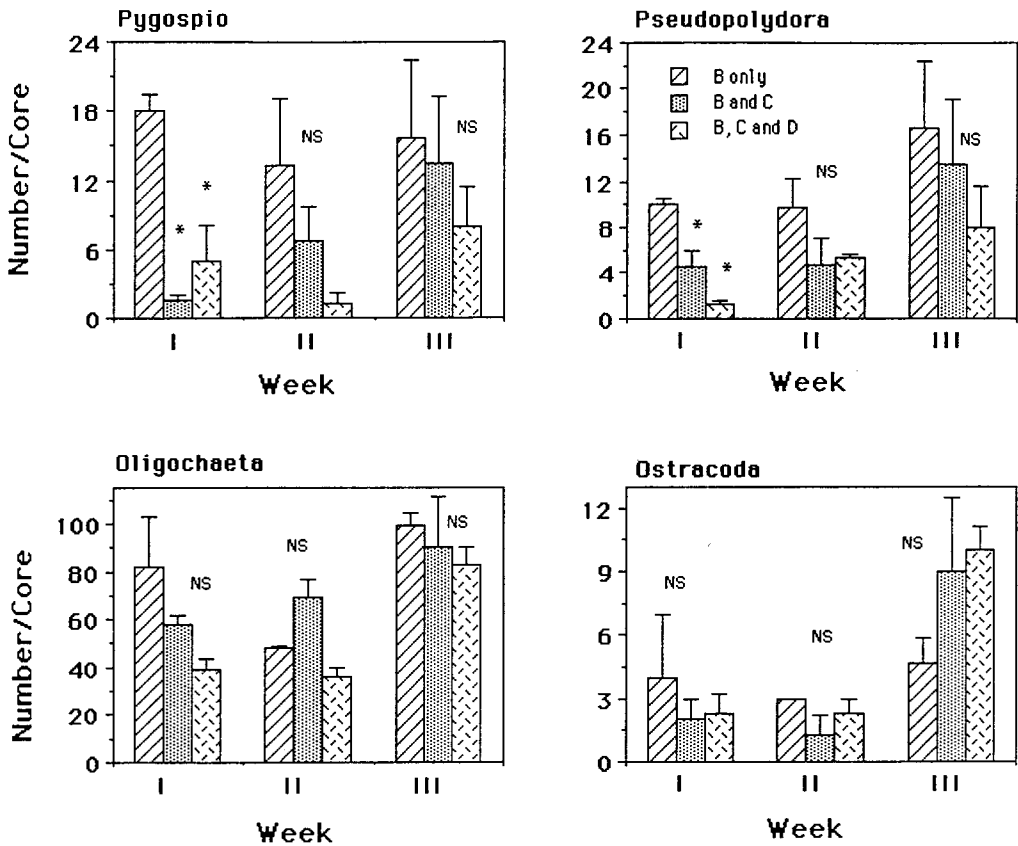


FIGURE 23.3. Results of analysis of the B rings (B core minus the inner A core) for the four major taxa in the 1-, 2-, and 3-week experiments. Means which share the same symbol are not statistically different ($p > .05$) but are different from any mean not sharing that symbol ($p \leq .05$). NS means that there is no statistical difference among any of the three means.

treatments. These data suggest that the presence of buffer zones of defaunated sediment (a C ring or a C and D ring) resulted in decreased adult recruitment; therefore, much of the colonization occurred by lateral migration. However, these patterns were not reflected in the Week 2 and Week 3 experiments where there were no significant differences among treatments. (It is perhaps notable that the nonsignificant trend of the means for the Week 2 and 3 experiments is consistent with immigration occurring laterally rather than vertically.) The same general pattern holds for *Pseudopolydora*. Significantly greater numbers were found in the B only treatment compared to the other two treatments in the Week 1 experiment, which did not differ from each other. However, no statistical differences were found in the Week 2 and Week 3 experiments although, as with *Pygospio*, the trends are in the direction that would be predicted by colonization by crawling laterally from unmanipulated sediment. For the infaunal oligochaetes and the epifaunal ostracodes, no significant differences were found among any of the treatments within each experiment.

Analysis of the pooled data by two-way ANOVA from all three experiments yields the results in Table 23.1. In all cases, the interaction term was nonsignificant, indicating that the two effects were orthogonal. The ANOVAs were recalculated, removing the interaction term from the model, and Scheffé post hoc contrasts were used to compare means among the experiments. The results of these contrasts are given in Figure 23.4. As shown in Fig. 23.4a, there were significantly more

Table 23.1. Results of two-way ANOVAs testing the effect of position (the area of defaunated sediment around the A cores and B cores) and duration (length of the experiment)

Analysis of A cores			
Species	Position	Duration	Position × duration
<i>Pygospio</i>	<i>a</i>	<i>b</i>	NS ^c
<i>Pseudopolydora</i>	NS	<i>b</i>	NS
Oligochaeta	NS	<i>b</i>	NS
Ostracoda	NS	<i>a</i>	NS

Analysis of B cores			
Species	Position	Duration	Position × duration
<i>Pygospio</i>	<i>a</i>	NS	NS
<i>Pseudopolydora</i>	NS	NS	NS
Oligochaeta	NS	<i>b</i>	NS
Ostracoda	NS	<i>b</i>	NS

^a $p \leq .001$.

^b $p \leq .01$.

^cNS - $p > .05$.

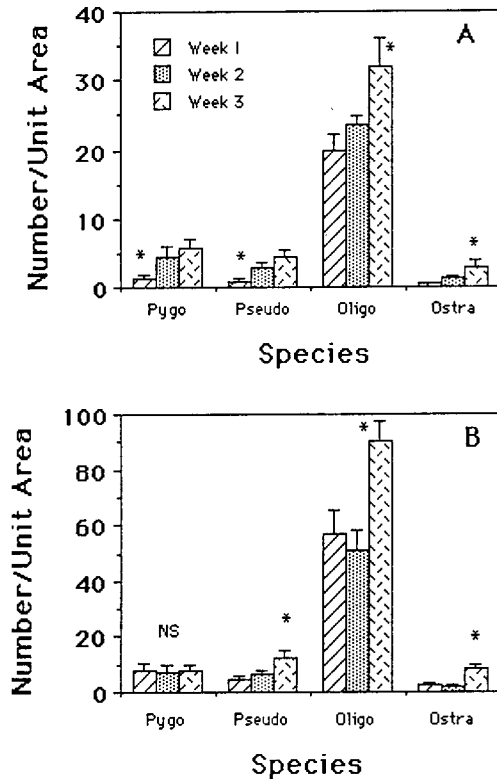


FIGURE 23.4. Comparison of the densities of each of the four major taxa as a function of time. A provides data for the A cores and B gives data for the B rings. Means which share the same symbol are not statistically different ($p > .05$) but are different from any mean not sharing that symbol ($p \leq .05$). NS means that there is no statistical difference among any of the three means ($p > .05$).

Pygospio found in the Week 2 and Week 3 experiments. The same pattern was found for *Pseudopolydora* with more animals found after 2 and 3 weeks compared to the 1-week experiment. For both oligochaetes and ostracodes, there was no difference in density between the 1- and 2-week means, but both were significantly less than the respective means for the 3-week experiment. The data also indicate that the rate of colonization differed among the taxa. For the A cores in the Week 3 experiment, *Pygospio* and *Pseudopolydora* had reached only 26.4 percent and 20.9 percent, respectively, of the natural densities. Oligochaetes reached 40.0 percent of ambient density after 3 weeks while ostracodes reached 43.7 percent of natural density. The same general pattern was obtained for the B areas: *Pygospio* and *Pseudopolydora* abundances within the experimental areas were only 10.2 percent and 16.5 percent, respectively, of ambient density after 3 weeks. Higher immigration rates by oligochaetes and ostracodes resulted in densities that were 150 percent and 100 percent of normal densities, respectively, by the end of 3 weeks. Although there were significant differences in the rates of colonization for the different species, there is a strong positive relationship between the number of colonizations and the length of time available for colonization (Fig. 23.4, Table 23.1).

Discussion

Many marine invertebrates display a complex life cycle in which the adult stage is benthic while a larval stage occurs in the plankton. The classic interpretation of such a life cycle (Thorson, 1950) ascribes a dispersal function to the larvae. Such a model works well for sessile, epifaunal organisms where adult dispersal is clearly impossible. For virtually all soft-sediment invertebrates living in a mobile substrate, some movement after settlement is possible. There is a considerable literature, mostly anecdotal in nature, indicating that adults of infaunal invertebrates may be encountered in the plankton (e.g., Costello, 1946; Dean, 1978a,b; Dauer et al., 1982). It is difficult to know from these accounts how frequent such forays into the water column are, although the estimate of a net export of 1.08×10^6 of infaunal invertebrates per day in the Lafayette River, Virginia (Dauer et al., 1982), suggests that the number of waterborne infauna can be appreciable. Recent experimental work with meiofauna has indicated that water currents can remove meiofaunal invertebrates from sediments into the overlying water column where passive dispersal occurs (Palmer, 1984, 1988a; Eskin and Palmer, 1985; Hicks, 1988). Other work on meiofauna has implicated disturbance by predators (Palmer, 1988b) and active dispersal into the water column (Service and Bell, 1987; Armonies, 1988).

The present research is an outgrowth of research that I performed in 1980 at the same site in False Bay. In the earlier work (Wilson, 1983), I placed small cylinders (28 mm in diameter) of insect screening (1 mm mesh) which had been filled with azoic sediment. In the laboratory, I systematically varied the number of *Pygospio* and *Pseudopolydora* in these cores before planting the cores into the sediment in the field. The densities of both species used were one-third normal density, normal density, three times normal density, and absence. Using all possible combinations of density, sixteen treatments were established. Experiments were run for 1, 2, 4, and 8 weeks. After 8 weeks, the densities of both spionids had converged to natural densities, indicating that emigration from the high-density treatments and immigration into the low-density treatments had taken place over the experimental time period. Furthermore, oligochaetes quickly colonized the experimental cores, achieving densities equal to natural densities within 8 weeks. I inferred from these results, with no direct evidence, that lateral movement of these organisms was occurring and suggested that the organisms could assess the local density around their tube or burrow but could not determine the density in other areas. If an infaunal organism had too many neighbors to allow

adequate resource acquisition, that organism should move and then reassess the density of organisms in its new neighborhood.

The present experiments were designed to gain insight into this adult dispersal process. It should be emphasized here that of the six common taxa in this community, only one, *Pseudopolydora*, has the "typical" marine invertebrate life cycle of benthic adults and planktonic larvae. In False Bay, *Pygospio* appears to reproduce entirely by asexual fragmentation (Wilson, 1985). The oligochaetes have direct development. The ostracodes have a nauplius larva in their life cycle, but the adults are highly dispersive themselves. Both *Corophium* and *Cumella* are peracarid crustaceans and hence brood their young to the juvenile stage.

The results of these experiments are surprising both in terms of the scale of dispersal and the mechanism of dispersal. For the A cores, the amount of defaunated sediment encircling the A core had no effect on the rate of colonization of the central area in eleven of twelve cases (Fig. 23.2). These data strongly indicate that the major route of colonization is from the overlying water column. If immigration were lateral, one would expect that A cores with less defaunated sediment around them should have significantly higher abundances of infauna than those with greater areas of surrounding defaunated sediment. It is important to note that the time-frame of the experiment was such that recolonization had not resulted in the attainment of natural densities for most taxa. Therefore, one cannot argue that migration had occurred by lateral movements but had occurred so quickly that the predicted effect of decreasing migrants with increasing total defaunated area was masked.

It was not surprising to find that the actively crawling ostracodes quickly colonized the defaunated areas. However, the rapid colonization by the oligochaetes was unexpected. These animals burrow beneath the sediment surface, and hence one would not predict that they would enter the water column frequently. However, the data clearly indicate that the route of colonization was from the water column. It is not possible to state with the present data whether the oligochaetes actively or passively entered the water column.

The data from the B areas (Fig. 23.3) agree with the data from the A cores. In ten of twelve cases, there was no significant difference among treatments, indicating that the primary route of immigration was from the water column rather than lateral migration from adjacent sediment. In the 1-week experiment, both *Pygospio* and *Pseudopolydora* showed higher densities in the B ring compared to the B-C and B-C-D ring, indicating that a significant amount of migration occurred by lateral movement of these spionids. However, these patterns were not seen in the 2- and 3-week experiments. In agreement with the A core analyses, the results from the B core experiments indicated that oligochaetes and ostracodes colonized at a much faster rate than either of the spionids. The data for oligochaetes and ostracodes strongly indicate that the primary route of colonization was from the water column.

The data from this study cannot distinguish between passive erosion of these invertebrates into the water column and active dispersal. My previous results (Wilson, 1983) showed that emigration by these taxa occurred in a density-dependent fashion, implying that these invertebrates actively choose to disperse. A review of the literature for other infaunal communities indicates a diversity of claims about the importance of active versus passive dispersal. Dobbs and Vozarik (1983) showed that storms can increase the number of waterborne infauna. Ambrose (1986) showed that the amphipod, *Rhepoxynius abronius*, emigrated via the water column in a density-dependent fashion. Floating behavior by the tellinid bivalve, *Macoma balthica*, has been described independently by Sörlin (1988) and Beukema and de Vlas (1989). These bivalves are stimulated to float by temperature and water currents.

Additional studies have demonstrated the importance of adult dispersal although it is not clear if emigration occurs in a density-dependent or density-independent fashion. Highsmith (1985) showed that infaunal invertebrates such as the tanaid crustacean, *Leptochelia dubia*, and the venerid bivalve, *Transennella tantilla*, can disperse by floating or algal rafting. Recolonization of the bottom of Tampa Bay after seasonal defaunation occurs in part by adult immigration (Dauer and Simon, 1976; Santos and Simon, 1980). None of these studies provided data on the relative importance of lateral versus vertical (waterborne) immigration.

In summary, it is apparent that the notion of dispersing larvae and sedentary adults fails to hold true for many infaunal invertebrates. Abundant evidence for the meiofauna indicate that waterborne dispersal of adults is common (e.g., Palmer, 1984, 1988a,b). For soft-sediment macrofauna, there is considerable evidence of adult dispersal (e.g., Levinton, 1979; Wilson, 1983; Ambrose, 1986). The present results, which are consistent with a vertical (waterborne) mode of adult dispersal, are surprising in light of the current dogma that tube-dwelling and burrow-dwelling infauna are sedentary (Woodin, 1974, 1976; Brenchley, 1981). It is clear that models of infaunal community structure will have to incorporate adult dispersal before useful predictions can emerge (Wilson, 1990).

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