

YALE PEABODY MUSEUM

P.O. BOX 208118 | NEW HAVEN CT 06520-8118 USA | PEABODY.YALE. EDU

JOURNAL OF MARINE RESEARCH

The *Journal of Marine Research*, one of the oldest journals in American marine science, published important peer-reviewed original research on a broad array of topics in physical, biological, and chemical oceanography vital to the academic oceanographic community in the long and rich tradition of the Sears Foundation for Marine Research at Yale University.

An archive of all issues from 1937 to 2021 (Volume 1–79) are available through EliScholar, a digital platform for scholarly publishing provided by Yale University Library at <https://elischolar.library.yale.edu/>.

Requests for permission to clear rights for use of this content should be directed to the authors, their estates, or other representatives. The *Journal of Marine Research* has no contact information beyond the affiliations listed in the published articles. We ask that you provide attribution to the *Journal of Marine Research*.

Yale University provides access to these materials for educational and research purposes only. Copyright or other proprietary rights to content contained in this document may be held by individuals or entities other than, or in addition to, Yale University. You are solely responsible for determining the ownership of the copyright, and for obtaining permission for your intended use. Yale University makes no warranty that your distribution, reproduction, or other use of these materials will not infringe the rights of third parties.



This work is licensed under a Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License.
<https://creativecommons.org/licenses/by-nc-sa/4.0/>



Flume experiments on post-settlement movement in polychaetes

by Karen I. Stocks^{1,2}

ABSTRACT

The ability of benthic polychaetes to move as adults and juveniles was examined using flume experiments. The main question asked was whether post-settlement movement is a passive process predictable from the hydrodynamic characteristics of the environment and the individual, or whether active behavior is involved. In one set of experiments, the percent of individuals moving during a six-hour period in low-food conditions was compared among five species of intertidal polychaetes. Flow speed was set at a velocity that did not cause sediment erosion but did cause bedload transport of anesthetized individuals. Species varied significantly in percent of movement, with *Laeonereis culveri*, *Nereis succinea* and *Lumbrineris tenuis* displaying negligible movement, *Polydora cornuta* having small but consistent movement, and *Streblospio benedicti* displaying the most movement (27% of individuals leaving original sediments in 6 h). Movement was not related to body size or mode of development, but showed a correlation with depth/feeding preferences: subsurface-feeders moved less than interface-feeders. Experiments with *P. cornuta* and *S. benedicti* that were extended to 18 hours indicated that post-settlement movement continued but the rate of movement during hours 6–18 was approximately half that during the first 6 hours. Experiments looking at the effects of experimental conditions on post-settlement movement in *S. benedicti* found that darkness had no effect, but that adding food, holding adults in still-water culture for 2.5 months, or growing larvae to adults in still-water cultures all significantly decreased movement. Overall, the results indicated an active component to post-settlement movement.

1. Introduction

Understanding and predicting dispersal and colonization is of continuing interest in soft-sediment benthic ecology. To date, the majority of work has focused on larvae as the dispersing mode of benthic macroinfauna. Clearly, planktonic larvae do serve a dispersal function (reviews by Scheltema, 1986; Butman, 1987; Underwood and Fairweather, 1989), and larval immigration is important in many recolonization events (e.g. Rhoads *et al.*, 1978; Levin, 1984a; Smith and Brumsickle, 1989; Shull, 1997).

A second dispersal mechanism is the movement of established benthic individuals (i.e., juveniles and adults). For the purposes of this paper we define “post-settlement movement”

1. Institute of Marine and Coastal Sciences, Rutgers University, 71 Dudley Road, New Brunswick, New Jersey, 08901, U.S.A.

2. Present address: San Diego Supercomputer Center, University of California, 9500 Gilman Drive/MC 0505, La Jolla, California, 92093-0505, U.S.A. *email: kstocks@sdsc.edu*

as the spatial redistribution of individuals having completed larval metamorphosis and undertaken a benthic existence (for simplicity, the term will also be applied to the movement of juveniles and adults of species lacking a free larval stage). Note that it is not restricted to recently settled individuals. The ability of adult and juvenile forms to transport actively or passively has been well documented as a frequent and widespread phenomenon (reviews by Gunther, 1992; Armonies, 1994; Palmer *et al.*, 1996). Evidence of post-settlement movement comes from finding post-settlement forms in water-column samples (e.g., Dean, 1978a; Cummings *et al.*, 1995; Olivier *et al.*, 1996b), in newly recolonized sediments (e.g., Bhaud *et al.*, 1981; Smith and Brumsickle, 1989; Wilson, 1994; Shull, 1997), and in sediment traps (e.g., Emerson and Grant, 1991; Turner *et al.*, 1997; Hunt and Mullineaux, 2002), or from documenting distribution changes over time in juveniles and adults (e.g., Beukema and de Vlas, 1979; Norkko *et al.*, 2001). In a review of the topic, Gunther (1992) found evidence of post-settlement movement in over 45 published studies that included gastropods, bivalves, amphipods, oligochaetes and both errant and sedentary polychaetes.

Some habitats, such as estuaries and salt marshes, have high proportions of direct-developing species (species lacking a larval stage for dispersal) (Bhaud and Duchêne, 1996; Giangrande, 1997). For these species, the movement of juveniles and adults is the only mechanism through which spatial dispersal and recolonization occurs.

Post-settlement movement has been more fully studied within some taxonomic groups than others. Within the mollusks, a series of field and laboratory flume studies has been used to conclude that several juvenile bivalves and gastropods drift using byssal threads to relocate after settlement, that this movement can occur below the organism's critical shear velocity, that in some species this ability is restricted to a particular juvenile stage, and that this movement can result in substantial redistributions of natural populations (e.g., Armonies and Hartke, 1995; Armonies, 1994; Baker and Mann, 1997; and references cited therein). To give one example, the redistribution of juvenile *Macoma balthica* in the Wadden Sea leads to predictable seasonal shifts in population locations (Beukema, 1973; Beukema and de Vlas, 1989). To give another, flume experiments demonstrated that adult bay scallops increase their emigration at both higher flows and higher conspecific densities (Powers and Peterson, 2000).

This study focuses on polychaetes, a common and abundant component of many soft-sediment marine communities. Within the polychaetes, only *Pectinaria koreni* has been studied adequately with both controlled, mechanistic experiments and field sampling to determine that post-settlement movement has an active behavioral component and that it results in substantial redistributions of populations in nature (Desroy *et al.*, 1997; Thiébaud *et al.*, 1998, and papers cited therein).

The majority of evidence for post-settlement movement in polychaetes is from field studies. Passive movement is suggested by research correlating increased post-settlement movement with increased flow or increased bedload transport of sediment (e.g., Dobbs and Vozarik, 1983; Olivier *et al.*, 1996b; Thiébaud *et al.*, 1996). However, active behavior is

suggested by a lack of correlation with hydrodynamics/sediment movement, changes in movement due to non-hydrodynamic forces such as day/night differences (Dean, 1978a) direct observation of swimming behavior (Dean, 1978b; Dauer *et al.*, 1980) or a combination of these factors (reviewed by Gunther, 1992; Armonies, 1994). Several community studies of post-settlement movement in the field have highlighted the likelihood of both active and passive mechanisms co-occurring (Armonies, 1994; Shull, 1997).

While such field data offer valuable indications that post-settlement movement exists and suggest the movement mechanism, flow fields in nature are complex and varying, and it is often impossible to determine whether individuals were passively eroded or actively migrated. Laboratory studies, particularly those that control flow with a flume, offer the ability to definitively separate passive erosion from active movement. To date, few such studies have been conducted on polychaetes. Olivier *et al.* (1996a) demonstrated for *Pectinaria koreni* that 85% of individuals tested left poor quality sediment (clean sand) at a flow below the critical shear velocity, though only 1% left a favorable, organic-rich mud. Wilson (1983) found that the emigration of *Pygospio elegans* in low-flow seawater tables increased with increasing densities of the competitor *Pseudopolydora kempfi* (Southern).

A second aspect of post-settlement movement in polychaetes that is poorly resolved is the mode of movement: do post-settlement polychaetes move along the sediment surface by crawling and bedload transport, or do they move in the water column. Studies finding increased recruitment into depressed defaunated plots (Savidge and Taghon, 1988) or decreased recruitment into raised defaunated sediment trays (Levin, 1984a; Smith and Brumsickle, 1989) implicate bedload transport as an important mechanism of post-settlement dispersal. However, planktonic collection of post-settlement stages implies water-column movement, as do observations of organisms actively swimming in the water column and the movement of some adults into raised trays (see Gunther 1992 for a review).

Differentiating between sediment-surface and water-column movement would help clarify the spatial scale on which post-settlement movement can influence the distribution of populations (Whitlatch *et al.*, 1998). Larval dispersal is known to act on a scale of up to hundreds of kilometers (Butman, 1987); the scale on which post-settlement dispersal can modify settlement patterns is not known.

The research presented here uses flume experiments on polychaetes to address two overarching questions. The first is whether the initiation of post-settlement movement in polychaetes is a purely passive hydrodynamic process or whether active behavior is involved. If organisms were simply eroded as passive particles, then post-settlement movement could be modeled using just the critical shear velocity of the sediments and the organism and the hydrodynamic regime of the habitat. If there is an active component, then models predicting post-settlement redistribution would need to include behavior. The second question addressed in this study is what is the mode of post-settlement movement. While flume results cannot determine the distances that polychaetes move in nature, they can indicate whether the method of initial movement is bedload or suspended-load transport (subsurface movement was not assessed). If post-settlement organisms are

transported in the water column or on surface films, they have the potential to move further than those crawling or in bedload transport.

These two general questions were examined in a suite of three controlled flume experiments. For all, the total degree of movement and the mode of movement (bedload or suspended-load) were examined. In the first set of experiments, five species of soft-sediment polychaetes were assessed. The passive-movement model predicts that no individuals would move at flow rates that do not cause erosion of the sediments. The species were chosen to represent a variety of developmental modes, feeding mechanisms, and depth preferences. When results did not conform to the null hypothesis of passive transport, then correlations with these factors were examined.

In the second set of experiments, the post-settlement movements of the two species that displayed consistent movement, *Streblospio benedicti* and *Polydora cornuta*, were examined over a longer time period. The purpose was to assess whether movement is restricted to the first few hours after individuals are placed in a new environment, or whether movement persists on a longer time frame of ~18 hours.

In the third set of experiments, movements of *Streblospio benedicti* were assessed under different conditions. Experiments were run in light vs. dark conditions, in food and no food treatments, and with individuals that had been collected recently from the field versus those that had been held in culture or raised from larvae in culture. Because these treatments did not change the hydrodynamic regime of the experiments, the null hypothesis of passive post-settlement movement predicts no treatment differences.

2. Methods

a. Experimental setup

All experiments were conducted in the racetrack flume at the Institute of Marine and Coastal Sciences, Rutgers University, New Jersey (<http://marine.rutgers.edu/flume/racetrk.html>; modeled after the flume described in Nowell *et al.*, 1989). Flow is driven by a repeating loop of paddles in one of the straight sections of the flume and is computer-controlled. Experiments were run in the other straight section, which is 630 cm long and 70 cm wide. For all experiments the flume was filled with 1 μm filtered natural seawater to a depth of 15 cm. Temperatures were between 18.5 and 20.5°C.

The general experimental protocol was to allow the polychaetes to burrow or build tubes in a sediment tray in the working straightaway of the flume and expose them to a set flow regime. A bedload trap—a vertical drop-slot 17.7 cm deep, 1.5 cm wide, and 43.5 cm in the cross-channel direction (aspect ratio of 11.8:1)—was set into the flume bottom 21.5 cm downstream of the sediment tray. This was designed to catch all organisms moving in bedload transport. Thirty cm downstream of the trap was a plankton net (200 cm long, 100 μm mesh) which filtered the entire cross section of the flume flow and was designed to collect all individuals in suspended-load transport. Observations of dye released at various levels in the water column indicated that the plankton net created few flow disturbances

other than a slight backflow of the surface film at high flow velocities. This backflow did not occur below the surface layer, and no organisms were ever observed near the water surface during experiments. No other eddies or disturbances were found. Dye paths also showed that the bedload trap disturbed water flow only within ~ 2 mm of the bottom.

The sediment tray was set into the flume so that the sediment surface was flush with the surrounding flume bottom. The tray was 3.2 cm deep with a surface area of 400 cm² and was divided into 4 equal compartments. For these experiments, the 4 tray compartments were treated identically and approximately equal numbers of individuals settled into each. For all experiments the sediment tray was filled with well-sorted, rinsed, olivine foundry sand (~ 90 μm diameter) that was smoothed flat. This sediment was within the range of grain sizes found in the natural habitats of all of these species, and was successfully used to culture all species. The tray was located 320 cm downstream of the channel bend, in a section where the boundary layer is fully developed and extends throughout the water column. The lateral variation in flow across the sediment tray is less than 5%. A light layer of sand was evenly sprinkled over the tray and trap area starting 2 m in front of the tray, to ensure that no flow disturbances were created when water encountered the trays.

On the day of the experiment, individuals were gently picked out of culture, examined to ensure they were undamaged, and settled into the sediment tray in the flume. To encourage worms to burrow into the sand, a vertical PVC tube (10 cm diameter) was placed over each tray compartment and a few drops of filtrate (0.7 μm glass fiber filter) was added to each from a slurry of seawater and natural mud taken from one of the field collection sites. Burrowing times for polychaetes can depend on sediment characteristics, and burrowing has been demonstrated to be slower in foundry sand than natural organic sediment (e.g., Woodin *et al.*, 1995). The filtrate was used in these experiments to hasten burrowing; initial tests showed that all species would burrow into the foundry sand without filtrate added, but at a slower rate. A filtrate was used instead of whole sediment to avoid adding a potential food source.

Worms were allowed a period of time (dependent on species, as described below) to burrow into the sediment and establish tubes. After this time, there was no observable change in the individuals' positions or tube characteristics. At the start of the experiment, any individuals not fully burrowed into the sand were removed.

b. Flow regime

Flow during the experiments approximated a 6.25 h half tidal-flow cycle, as might be experienced during an ebb or flood in a tidal creek or intertidal flat. The maximal velocity was selected to produce a u^* of ~ 0.33 cm s⁻¹ as calculated from Laser Doppler Velocimeter profiles of vertical velocity (Nowell *et al.*, 1981). This equated to a velocity of 11 cm s⁻¹ measured at 10 cm above the sediment ($\pm < 5\%$ in cross-channel variation). This flow rate is considered a moderate one in nature; it is often regularly exceeded during peak tidal flows in the mudflat and marsh tidal creek habitats in which these species live (e.g., Roman, 1984; Reed, 1988; Suk *et al.*, 1999; Janssen-Stelder, 2000; Le Hir *et al.*,

Table 1. Characteristics of species used in flume experiments. Length indicates the range of body lengths used. Development modes are taken from Giangrande (1997); Lec. larv. = lecithotrophic larvae; Direct = direct development; Plk. Larv. = planktotrophic larvae. Sources for feeding modes are: *Lumbrineris tenuis*—Fauchald and Jumars (1979); *Laeonereis culveri*—Mazurkiewicz (1975); *Nereis succinea*—Fauchald and Jumars (1979); *Polydora cornuta*—Dauer *et al.* (1981); *Streblospio benedicti*—Levin (1984b). Depth zone refers to primary feeding depth (“surface” includes deposit- and suspension-feeding).

Species	Length (mm)	Fall velocity	Age class	Mode of development	Mode of feeding	Depth zone
		± std. dev.				
<i>Lumbrineris tenuis</i>	15–35	1.41 ± 0.37	Subad./Adult	Lec. larv.	Omnivore	Subsurface
<i>Laeonereis culveri</i> —Sm	5–8	0.84 ± 0.27	Juvenile	Direct	Herbiv./Omniv.	Subsurface
<i>Laeonereis culveri</i> —Lg	15–30	1.89 ± 0.35	Subad./Adult	Direct	Herbiv./Omniv.	Subsurface
<i>Nereis succinea</i>	15–30	1.94 ± 0.61	Subad./Adult	Plk. larv.	Omnivore	Subsurface
<i>Polydora cornuta</i>	4–12	1.45 ± 1.00	Adult	Direct/Plk. larv.	Deposit/Suspension	Surface
<i>Streblospio benedicti</i>	4–12	0.95 ± 0.54	Adult	Lec. larv.	Deposit/Suspension	Surface

2000; Uncles and Stephens, 2000). This particular shear level was selected because it caused no sand transport but did transport inert polychaetes on the sediment surface through bedload transport. Trials with *Streblospio benedicti* killed in two ways (immersion in ethanol and prolonged immersion in a $MgCl_2$ narcotic solution) indicated this shear was well below the critical level for the bedload transport of unburied individuals. In all tests where individuals were killed and placed on the tray surface and exposed to this flow velocity, all individuals were recovered from the trap. None were suspended and recovered in the net, and none failed to move. Other species were not tested, but fall velocities of all species were measured for comparison with *S. benedicti* (individuals anesthetized with $MgCl_2$ solution were timed through known distances as they fell through a graduated cylinder of still seawater) (Table 1).

The flow program began with 15 minutes of a low flow (28% of the maximum—a level that did not cause transport of inert individuals). It then increased by ~4% every 3 minutes up to the maximum. It remained at the maximum for the bulk of the program (5 h), then slowed down over 6 minutes to 28% of the maximum for another 15 minutes.

Because the flow did not cause sediment erosion, any individual recaptured in the sediment trap or net after an experimental run must have actively moved to the sediment surface (at the start of the experiments, all individuals were burrowed into the sediment). And because inert individuals on the sediment surface moved in bedload transport and not suspended-load transport, any individual recaptured in the plankton net must have exhibited active swimming.

Because the small movements of a person watching the flume caused some of the species used to withdraw into the sediment, the experiments were not continually observed (a video system was unavailable). For this reason, observations of the behavior of moving polychaetes are not available. Each experiment was checked several times during each 6 h

Table 2. Details of flume experiments conducted. Those runs marked with an asterisk were conducted over 3 flow cycles of 6.25 h, the remainder were conducted over 1 cycle.

Species	Treatment	Runs	# Indiv. per run (in 400 cm ² tray)
<i>Lumbrineris tenuis</i>	Standard	3	25, 31, 27
<i>Laeonereis culveri</i> —Sm	Standard	2	29, 30
<i>Laeonereis culveri</i> —Lg	Standard	2	15, 8
<i>Polydora cornuta</i>	Standard	3	34*, 20, 30*
<i>Nereis succinea</i>	Standard	3	20, 19, 20
<i>Streblospio benedicti</i>	Standard	6	37*, 34*, 46*, 40*, 30*, 42*
<i>Streblospio benedicti</i>	Algae added	5	38*, 35*, 41*, 46*, 29*
<i>Streblospio benedicti</i>	Dark	4	31*, 38*, 37*, 33*
<i>Streblospio benedicti</i>	Held in culture	4	36*, 31*, 40*, 32*
<i>Streblospio benedicti</i>	Raised from larvae	4	37*, 40*, 41*, 38*

cycle, and those polychaetes visible in the sediment trap were noted, though because all individuals could not always be seen in the trap these in-progress counts are not reported.

The above gives the standard protocol for all experiments. The details of each set of experiments are described below, and departures from this protocol noted.

c. Experiment 1: Species comparisons

In this set of experiments, the movement behaviors of five species of intertidal polychaetes were assessed: the lumbrinerid *Lumbrineris tenuis*, the nereids *Laeonereis culveri* and *Nereis succinea*, and the spionids *Polydora cornuta* and *Streblospio benedicti*. Tables 1 and 2 give details of the experimental runs and size ranges for each species; note that two size classes of *L. culveri* were used. Only one species was used per experimental run, and brooding individuals and heteronereids were not used.

All individuals were collected from the local New Jersey shore a maximum of 12 days before the experiment. *Laeonereis culveri* came from a mudflat in the Hackensack Meadowlands (40.784N, 74.125W); all other species were collected from the intertidal area of Shark Bay Inlet (40.187N, 74.009W). *S. benedicti* is known to have two, genetically-determined modes of reproduction—planktotrophic and lecithotrophic—which can be differentiated by larval morphology and the brood characteristics of gravid females (Levin, 1984b). The lecithotrophic form was used in this study. While both forms were present at the collection site, the planktotrophic one was less common and local patches tended to contain either one or the other almost exclusively. Therefore, though non-gravid adults could not be individually assessed, examination of the co-occurring gravid females gave a good indication of the reproductive mode shared by individuals in the patch. This was confirmed by holding non-breeding adults in culture long enough for juvenile females to become gravid.

Individuals were kept for at least two days before the experiments in still-water culture

dishes at 15°C with plentiful food. The deposit-feeding spionids were given natural sediment that had been frozen and sieved through a 300 µm mesh and enriched with algal paste. *Laeonereis culveri*, a jawed herbivore (Mazurkiewicz, 1975), was given the same sediment plus chopped spinach. The predatory species, *Lumbrineris tenuis* and *Nereis succinea*, were given small amounts of unfrozen native sediment containing live fauna. Cultures of all species were successfully continued using these methods for at least four weeks with low mortality and individuals looking healthy for the entire period.

The time allotted before a flume run for each species to burrow into the sediment tray and establish tubes or burrows varied, but was always between 1.5 and 4 h. Individuals of the two Spionid species were added at intervals of 1–2 minutes and allowed 1.5 h to establish. The establishment time was sufficient for at least 75% of individuals to burrow. The more aggressive Laeonereid and Nereid species were added individually and each allowed to burrow fully before adding the next in order to avoid interactions between individuals—this led to longer total establishment times of 3–4 h. After this time, there was no observable change in the individuals' positions or tube characteristics. Any individuals not burrowed into the sediment were removed before the experiment began. The density of individuals used also varied by species (Table 2), but was always on the low end of the range of reported field densities for these species (Stocks, 2000, 2001).

These experiments were run for one 6.25 h flow cycle. At the end of the experiment, individuals were collected from the sediment tray, bedload trap, and plankton net (the other flume surfaces were also checked, but no individuals were ever found).

d. Experiment 2: Extended experiments

These experiments were run to determine if movement was restricted to an initial period, or whether it continued over time. Two species were used: *Polydora cornuta* and *Streblospio benedicti* (Table 2—those runs marked with an asterisk). The experimental conditions were identical to Experiment 1 except that each run was extended for a three flow cycles. During the low flow period between the first and the second cycle, individuals in the bedload trap and the plankton net were removed and counted. At the end of the third cycle, individuals were recovered from the sediment tray, bedload trap, and plankton net. The total experimental duration was 18.75 hours (three 6.25 h cycles), but for simplicity the time periods will be referred to throughout as 0–6 and 6–18 h. The flume was not sampled between the second and third cycles; data are available for movement during the 0–6 h period and the 6–18 h period. Note that for these extended experiment the results from the initial 0–6 h cycle are reported in Experiment 1.

e. Experiment 3: Effects of experimental and culturing conditions

In these experiments, the movements of *Streblospio benedicti* under 4 different experimental and pre-experimental conditions were compared to a standard treatment (Table 2). The standard treatment is that used for Experiments 1 and 2: filtered seawater, room lights

on, and individuals used within 12 days of field collection. All runs were conducted over three flow cycles.

In “dark” treatments, the entire flume channel except for the paddle area was wrapped with heavy, black, plastic sheeting. Measurements with a LI-COR Li-1000 light meter with spherical quantum sensor indicated that ambient light levels above the sediment tray were below the detection level of the instrument ($3 \mu\text{A}$ per $1000 \mu\text{mols}^{-1} \text{m}^{-2}$).

In “algae added” treatments, 70 ml of a concentrated commercial algal slurry containing mixed phytoplankton species (“C6” from Coast Seafoods Co., 12951 Bel-Red Road, Bellevue, Washington, USA) was added to the water column to produce a final concentration of $\sim 3,000$ cells/ml. This is in the range of concentrations found in phytoplankton blooms in estuarine and coastal waters. Similar concentrations of this slurry have produced relative growth rates as high as 30% per day for *S. benedicti* in flume experiments (Hentschel, 1999), indicating that it is an accessible food source.

In “cultured” experiments, larvae from gravid wild-caught females were raised in still-water culture for 9–12 weeks. The length of culture time was determined by the development rate: worms grown in culture from larvae were not used until they reached the adult size of 4+ mm and gravid females were observed in the culture. Cultured worms were held at 15°C with irregular light and fed with plentiful sieved sediment and algal paste. Using these methods, *S. benedicti* were successfully reared through several successive generations, though only the first generation was used in experiments.

In “held” experiments, individuals that were collected as adults from the field were held in still cultures with food for 9–13 weeks. The conditions and food were as for the “cultured” treatment.

f. Statistical analysis

For Experiment 1 (species comparisons), the total percent of movement for the 5 polychaete species is reported. Statistics were not conducted because the only two species displaying consistent movement were used for the extended Experiment 2 runs. The 0–6 h results reported in Experiment 1 for these species are a subset of the results reported in Experiment 2, and are analyzed there.

For Experiment 2 (extended experiments), the rates of total movement (net plus trap) were compared between the 0–6 and 6–18 h treatments for each species separately using paired 2 sample t-tests with experimental runs as replicates. The percentages moving during the 6–18 h part of the experiments were calculated based on the numbers remaining in the tray at the 6 h time point. To determine whether bedload transport or suspended load transport was significantly higher for *S. benedicti* (the only species with net captures), the percentages recovered in the trap versus the net over the entire 0–18 h period were compared using t-tests (experimental runs were replicates).

For Experiment 3 (experimental conditions), the effects of darkness, algae addition, holding in culture for ~ 2.5 months, and rearing from larvae in culture on the movement of *Streblospio benedicti* was determined by comparing each treatment to the “standard”

treatment (recently collected worms run in light with no algae added). For each treatment, the percent moving (trap plus net) in the 0–6, 6–18 and 0–18 h periods were compared to the standard, with runs as replicates. Because several of the treatments did not meet normality assumptions even with transformations, Wilcoxon Rank Sum Tests (equivalent to Mann-Whitney Rank Sum tests) were applied with corrections for continuity and ties. Within each treatment, the percent found in the net versus the trap during the 0–6, 6–18, and 0–18 h period were similarly compared, but because none of these comparisons were significant comparisons were not made to the standard treatment.

All statistical tests were conducted using Statistix 7 software from Analytical Software (<http://www.statistix.com>). Results were considered statistically significant at $P < 0.05$.

Because individuals in runs that were not designated as cultured were used within a range of 2 to 12 days after collection, an unweighted least squares linear regression was calculated for total percent movement vs. number of days since collection for the standard runs of *S. benedicti* (the longest-held species—individuals of all other species were used within 7 days) to determine if holding on this time scale affected movement.

3. Results

a. Experiment 1: Species comparisons

The five species exhibited different degrees of movement (Fig. 1). *Lumbrineris tenuis* and both large and small *Laeonereis culveri* showed no movement—100% of individuals were recaptured in the original sediment trays. For *Nereis succinea*, one individual (of 59 tested over three experiments) was recaptured in the bedload trap. *Polydora cornuta* had consistent but low levels of movement: in each of the three runs, at least one individual was recaptured from the trap for an average of 7.1% movement, and an average rate of $1.1\% \text{ h}^{-1}$. *Streblospio benedicti* displayed the most post-settlement movement, with an average of 26.9% moving during the six-hour experiment ($4.3\% \text{ h}^{-1}$). During most experiments all individuals were accounted for at the end of the experiment. The exception is that in three of the *S. benedicti* experiments a total of 4 individuals were not recaptured, which represents 2% of the total individuals used.

b. Experiment 2: Extended experiments

During the 6–18 h interval, movement occurred consistently in *P. cornuta* and *S. benedicti* runs (Fig. 2) (18-h experiments were not conducted on the other species). Note that the time period of the second interval is twice as long as the first interval, so that similar percent movements translate into substantially different rates of movement. An average of 24.3% of *S. benedicti* and 6.3% of *P. cornuta* (of those left in the tray at hour 6) moved in the second sampling interval. This is equivalent to a movement rate of $1.9\% \text{ h}^{-1}$ for *S. benedicti* and $0.5\% \text{ h}^{-1}$ for *P. cornuta* during the 6–18 h period, versus 4.3% and $1.1\% \text{ h}^{-1}$, respectively, for the 0–6 h period. Movement was significantly lower during the second interval for *S. benedicti* ($P = 0.022$), but not for *P. cornuta* ($P = 0.992$), though

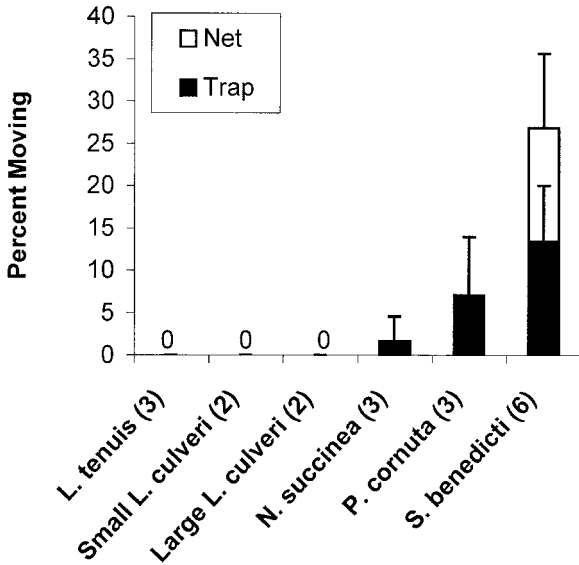


Figure 1. Average percent of individuals leaving sediment tray during the initial ~6 h flow cycle, divided into the percent of individuals recaptured in the plankton net and the sediment trap. The number of runs per species is indicated in parentheses on the x-axis. Error bars are applied to the net and trap components (not the total percent), and are calculated as the standard deviation between runs.

resolution was low for *P. cornuta* because only 2 runs were successfully carried out over 18 h (versus 6 for *S. benedicti*).

The mode of movement was further examined for *Polydora cornuta* and *Streblospio benedicti* (Fig. 2). In *P. cornuta*, all of the moving individuals (a total of nine) were recaptured from the bedload trap—none were found in the plankton net. *S. benedicti* was the only species recaptured in the plankton net. For *S. benedicti*, the numbers recaptured in the plankton net versus bedload trap were approximately equal (56.3% in the net vs. 43.7% in the bedload trap as calculated for the entire 0–18 h interval; not a significant difference statistically), but the variability between experiments was high (a range of 25–78% for net recaptures over the 6 experimental runs). During checks of in-progress experiments the number of individuals observed in the bedload trap never decreased, indicating that movement out of the trap once captured was rare or absent.

c. Experiment 3: Effects of experimental conditions on *Streblospio benedicti*

Dark. The total percent of *Streblospio benedicti* moving was not significantly affected by light conditions (Fig. 3, Table 3). 43.4% moved during the 18 h experiment in darkened flumes in comparison with 44.6% in the standard full-light treatment. Nor were significant differences seen when the 0–6 h and 6–18 h intervals were considered separately. Proportions recaptured in the net vs. trap were not significantly different.

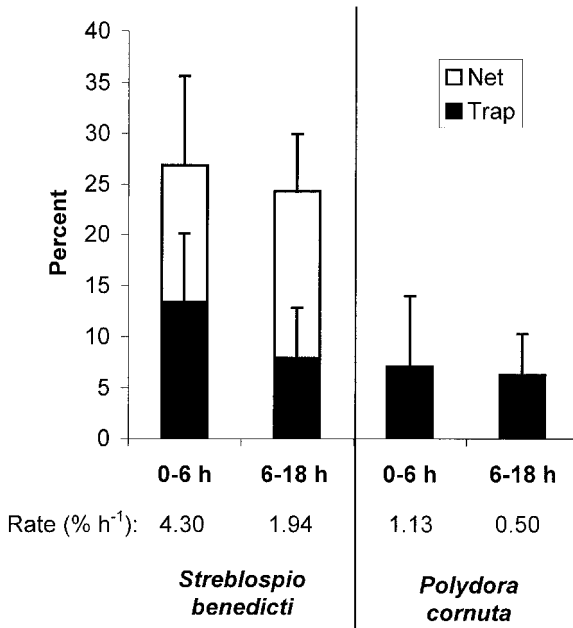


Figure 2. Average percent of individuals moving during the 0–6 and 6–18 h segments of extended flume runs, divided into the percent of individuals recaptured in the plankton net and sediment trap. Error bars of one standard deviation are applied to the net and trap components (not the total percent). The rate of movement, in % per hour, is given for each species and time period: note that the second time interval is twice as long as the first, so that an equal *percent* movement in the 6–18 h interval as the 0–6 h interval indicates a *rate* of movement that is half as large.

Algae added. Algae addition did affect *Streblospio benedicti* movement: total movement averaged 26.1% over 18 h in experiments with algae added compared to 44.6% in standard conditions (Fig. 3) and this difference was highly significant (Table 3). While this effect was not statistically significant for the 0–6 and 6–18 h intervals when considered separately, the trend of decreased movement with algae addition was consistent. No significant differences in the percent recaptured in the net versus the trap were found in the total experiment or for any individual time interval.

Held and cultured. Total percent movement was significantly decreased both in *Streblospio benedicti* held in still cultures for 9–12 weeks and those reared from larvae in still cultures compared to recently-collected individuals (Table 3, Fig. 3). Overall, the average percent moving during the whole experiment was 6.0% and 8.2% in held and reared-from-larvae treatments, respectively, compared to 44.6% in the recently-collected standard treatment. This effect was significant for both the 0–6 and the 6–18 h intervals when considered separately.

Holding in still-culture on the timescale of 2–12 days (the range for individuals in the “standard” experiment) had no effect on the total movement of *S. benedicti* ($F = 0.03$, $P = 0.88$).

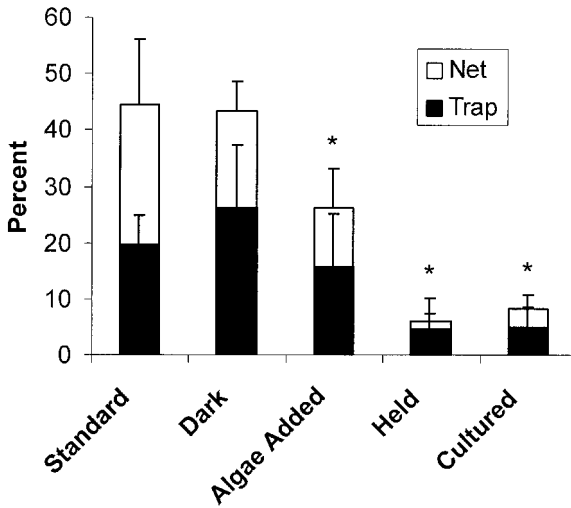


Figure 3. Total percent of *Streblospio benedicti* moving under different flume conditions during 18 h experiments, divided into the percent of individuals recaptured in the plankton net and sediment trap. Error bars of one standard deviation are applied to the net and trap components (not the total percent). Asterisks (*) indicate significant differences in total percent movement from standard conditions.

4. Discussion

The main purpose of this set of experiments was to test the null hypothesis that post-settlement movement in the polychaetes examined is a purely passive process driven by hydrodynamics. While active movement behavior in polychaetes has been demonstrated or suggested by a variety of field studies (e.g., Dean, 1978a, b; Dauer *et al.*, 1980; and reviews by Gunther, 1992; and Armonies, 1994) few experiments have been conducted in which flow is known definitively enough to separate active from passive movements. The results presented here supplement the findings of active movement in Olivier *et al.*'s (1996a) flume study on *Pectinaria koreni*, in which significantly more individuals left

Table 3. Results of Mann-Whitney *U* tests for treatment effects on the percent movement (sum of recapture from bedload trap and plankton net) of *Streblospio benedicti* in flume experiments.

Treatment	Total		0-6 h		6-18 h	
	U	P	U	P	U	P
Dark	13	0.915	14	0.749	12.5	0.915
Algae	27	0.035*	24	0.121	25	0.080
Held in culture	24	0.014*	23	0.025*	24	0.014*
Raised in culture	24	0.014*	23	0.025*	24	0.014*

* indicates significance at *P* < 0.05.

poor-quality sediment than high-quality sediment, and Wilson's (1983) finding of increased emigration of *Pygospio elegans* with increased densities of a competitor in near-still laboratory experiments.

a. Species comparisons

The results of the inter-specific comparisons reported here contradict the hypothesis of passive movement, and indicate a role for active behavior. Because experiments on all species were conducted at a flow below the critical threshold for sediment erosion to begin, and because all individuals were beneath the sediment interface at the start of each experiment, the fact that movement was found (Fig. 1) negates the model of post-settlement movement as a purely passive erosion process. Any movement out of the sediment tray must have involved, at a minimum, the individual exiting the sediment and moving to the sediment-water interface.

The five species tested varied in their degree of post-settlement movement (Fig. 1). This variation could not be explained the physical size or fall velocities of the polychaetes used (Table 1). For example, *Streblospio benedicti* and small *Laeonereis culveri* had similar fall velocities and size ranges, yet the former displayed high movement while the latter displayed none. Neither did it relate to the reproductive mode of the species: direct developers (species without a planktonic dispersal stage) did not exhibit more post-settlement movement than those with one (Table 1, Fig. 1). Of the species used, *Laeonereis culveri* was a direct developer and displayed no movement. Both *Lumbrineris tenuis* and *Streblospio benedicti* have lecithotrophic larvae and one displayed no post-settlement movement while the other displayed the highest degree of movement.

Post-settlement movement did show a potential relationship to the feeding mode and/or depth distribution of the species (Table 1, Fig. 1). Both of the species with consistent movement, *Streblospio benedicti* and *Polydora cornuta*, use palps to either deposit- or suspension-feed at the sediment-water interface. The remainder of the species are mainly subsurface feeders including herbivores (*Laeonereis culveri*) and omnivores (*Lumbrineris tenuis* and *Nereis succinea*). Results from the algae addition experiment with *S. benedicti* indicate that it is unlikely that the physical act of extending palps into the boundary layer to feed caused deposit and suspension feeders to be passively eroded: individuals in the algae added treatment were less likely to move than those in the filtered-water treatment, yet they were observed to be feeding more actively.

One possible explanation for the importance of depth is that subsurface feeders, which must move frequently to find new food resources, may rely more on subsurface burrowing to change location. This form of movement would not have been seen in these experiments, because the sediment trays had solid sides. Surface-feeders, which build more permanent tubes and can have a fresh supply of food brought by currents, may not be as adept at subsurface motion (though they are physically capable of subsurface movement, pers. obs.) and thus use bedload and suspended-load transport more. Alternatively, subsurface feeders may be less sensitive to a lack of food on this timescale.

b. Timescale of movement

The experiments that were extended over three flow cycles (18 h) with *Polydora cornuta* and *Streblospio benedicti* give some indication of the temporal characteristics of post-settlement movement. For both species, movement continued in the 6–18 h period (Fig. 2), indicating that post-settlement movement was not simply a short-term reaction to disturbance. This is supported by casual observations made during flume experiments that individuals appeared in the trap fairly regularly throughout the experimental runs—a majority of movement was not seen, e.g., in the first hour or so of the experiment. The overall rate of movement, however, did decrease significantly in *S. benedicti*, with the percent movement per hour in the 6–18 h period about half of that during the initial 0–6 h period (because the second period lasted twice as long as the first, the approximately equal total percent movements in the two periods represent different rates of movement).

c. Effects of experimental conditions past and present

The third set of experiments tested for active versus passive movement by varying conditions that were unrelated to the hydrodynamic regime in the flume and comparing the subsequent movement of *Streblospio benedicti* adults. Because significant treatment differences were found (Fig. 3, Table 3), the model of passive movement is again rejected. Light versus dark conditions had no effect, but experiments run with food (algal slurry) added to the water had significantly less movement than the “standard” runs with filtered water. For *S. benedicti*, a deposit- and suspension-feeder, the “standard” experimental conditions represent an impoverished food environment (both sets of experiments used a clean foundry sand for the substrate).

Instead, the results are consistent with behaviorally-mediated, active movement in *Streblospio benedicti*. They also conform to the predictions of optimal foraging theory: individuals were more likely to move when in poor food conditions than good ones (MacArthur, 1972). Olivier *et al.* (1996a) found a similar pattern in flume experiments with the polychaete *Pectinaria koreni* run with favorable and unfavorable sediment. If this behavior holds for field conditions, it indicates that *S. benedicti* may actively move from poor-quality environments after settlement. Though the food level represented in the standard conditions may be lower than that found in the natural environment of this species, the results indicate both the potential for this species to move and the fact that food likely affects it. What the shape of the food-movement relationship is, and how it plays out in nature, are questions that must be addressed by further research.

Given that conditions such as low food resources increased post-settlement movement in one polychaete species from this study, and also in the species studied by Olivier *et al.* (1996a), caution is advisable when extrapolating up from small scale experiments to large-scale effects. The results from, for example, caging studies of predation and competition may not extrapolate to population-level effects if individuals can escape locally poor conditions.

The results from the cultured vs. recently-caught experimental runs indicate that

post-settlement movement behavior reflects past as well as present conditions. In the species used, *Streblospio benedicti*, post-settlement movement was significantly decreased in well-fed, still-water-cultured individuals (Fig. 3, Table 3). This applied not just to those that were grown from larvae in culture over 9–13 weeks (“cultured”), but also to those collected as adults and held in culture for 9–12 weeks (“held”). I am not aware of other research examining changes in post-settlement movement behavior under different pre-experimental conditions.

These experiments could not distinguish the cause of differential response in culture-held *Streblospio benedicti*. It is possible that post-settlement movement relates to an endogenous cycle requiring environmental cues, such as tidal or daylight cycles, to persist. Alternatively, movement may relate to conditions integrated over some time period. Thus individuals experiencing several weeks of high food, predator-free conditions in culture may be less likely to move within a short time in unfavorable flume conditions than those recently collected from less-favorable field conditions. Internal nutritional state is one possible stimulus for such movement.

Because adults held in culture and larvae reared in culture responded similarly, post-settlement movement behavior is not fixed at a certain stage in development but retains some plasticity. While these experiments were not designed to test the “critical timescale” of the change in movement response, because no effect of movement was found for holding on timescales of up to 12 days, it appears that the holding effect impacts individuals held for longer than 12 days and less than ~2.5 months. These results are a caution for researchers: cultured organisms may not be appropriate for behavior experiments involving flow.

d. Conclusions and implications

Overall, the results of these three experiments indicate that post-settlement movement in polychaetes is not a purely hydrodynamic erosion process, but one that involves active behavior and is mediated by conditions both past and present. Studies seeking to understand redistribution patterns in nature may require more complex models than simple hydrodynamic ones. The experiments also demonstrate that the potential magnitude of post-settlement movement varies among species, but can be quite high: in certain low-food conditions almost 45% of *Streblospio benedicti* moved in an 18-h period when exposed to natural flow levels (e.g., Roman, 1984; Reed, 1988; Suk *et al.*, 1999; Janssen-Stelder, 2000; Le Hir *et al.*, 2000; Uncles and Stephens, 2000). Olivier *et al.* (1996b) found rates of movement from unfavorable sediments of 85% for the polychaete *Pectinaria koreni*. Furthermore, approximately half of the movement recorded here for *S. benedicti* was by water-column transport, a movement vector with the potential to distribute individuals further than bedload transport.

Post-settlement movement therefore represents a potentially large vector for redistribution. How this potential is displayed in nature is not resolved by these experiments. While a variety of evidence exists indicating post-settlement movement occurs in nature (reviewed

in Gunther, 1992), too few field studies of recolonization events have been done with frequent enough sampling and fine enough sieve sizes to track larval versus post-larval immigration effects on recolonization trajectories. Further field experiments using techniques such as those developed by Whitlatch and Osman (1998) for frequent sampling during recolonization, would inform this debate.

Furthermore, estimating numbers of larval settlers versus post-settlement immigration is not a complete answer. It is possible that post-settlement colonization may have an importance for recolonization out of proportion to the numbers of individuals: mortality is likely higher for recently-settled larvae than adults (Forbes and Lopez, 1990) and the presence of adults may alter the ability of larvae to settle and recruit (e.g., Gallagher *et al.*, 1983; Thrush *et al.*, 1992; Woodin *et al.*, 1995). A scale-dependent recolonization model by Whitlatch *et al.* (1998) indicates that patch recovery may be very sensitive to rates of post-settlement juvenile immigration. Experiments in a variety of habitats, particularly those such as salt marshes in which a high proportion of infauna lack planktonic larvae (Bhaud and Duchêne, 1996), tracking the growth and survival trajectories of larval, juvenile, and adult immigrants into recolonizing areas could indicate the relative importance of these dispersal modes to community structure.

Acknowledgments. The author gratefully acknowledges the advice and input of Judith Grassle, Jean Marie Hartman, Gary Taghon, Sybil Seitzinger, Brian Hentschel and especially J. Frederick Grassle during the planning and writing of this study. Char Fuller and Piotr Nawrot at the flume facility of the Institute of Marine and Coastal Sciences gave generously of their time to facilitate the mechanics of the experiments. The unflinching laboratory assistance of Jen Gregg and Pat McGrath are also appreciated. This work was supported by EPA STAR Fellowship U914949-01-2 and a Research Assistantship from the Graduate Program in Oceanography at Rutgers University.

REFERENCES

- Armonies, W. 1994. Drifting meio- and macrobenthic invertebrates on tidal flats in Köningshafen: a review. *Helgol. Meeresunters.*, *48*, 299–320.
- Armonies, W. and D. Hartke. 1995. Floating of mud snails *Hydrobia ulvae* in tidal waters of the Wadden Sea, and its implications in distribution patterns. *Helgol. Meeresunters.*, *49*, 529–538.
- Baker, P. and R. Mann. 1997. The postlarval phase of bivalve mollusks: a review of functional ecology and new records of postlarval drifting of Chesapeake Bay bivalves. *Bull. Mar. Sci.*, *61*, 409–430.
- Beukema, J. J. 1973. Migration and secondary spatfall of *Macoma balthica* (L.) in the western part of the Wadden Sea. *Neth. J. Sea Res.*, *23*, 356–357.
- Beukema, J. J. and J. de Vlas. 1979. Population parameters of the lugworm *Arenicola marina*, living on tidal flats in the Dutch Wadden Sea. *Neth. J. Sea Res.*, *13*, 331–353.
- 1989. Tidal-current transport of thread-drifting postlarval juveniles of the bivalve *Macoma balthica*. *Mar. Ecol. Prog. Ser.*, *52*, 193–200.
- Bhaud, M., D. Aubin and G. Duhamel. 1981. Recrutement du substrat en larves d'invertébrés: rôle de l'hydrodynamisme. *Oceanis*, *7*, 97–113.
- Bhaud, M. and J. Duchêne. 1996. Change from planktonic to benthic development: is life cycle evolution an adaptive answer to the constraints of dispersal? *Oceanol. Acta*, *19*, 335–346.
- Butman, C. A. 1987. Larval settlement of soft-sediment invertebrates: The spatial scales of pattern

- explained by active habitat selection and the emerging role of hydrodynamic processes. *Oceanogr. Mar. Biol. Ann. Rev.*, *25*, 113–165.
- Cummings, V. J., R. D. Pridmore, S. F. Thrush and J. E. Hewitt. 1995. Post-settlement movement by intertidal benthic macroinvertebrates: do common New Zealand species drift in the water column? *N.Z. J. Mar. Freshwater Res.*, *29*, 59–67.
- Dauer, D. M., C. A. Maybury and R. M. Ewing. 1981. Feeding behavior and general ecology of several spionid polychaetes from the Chesapeake Bay. *J. Exp. Mar. Biol. Ecol.*, *54*, 21–38.
- Dauer, D. M., G. H. Tourtellotte and H. R. Barker. 1980. Nocturnal swimming of *Scolecopides viridis* (Polychaeta: Spionidae). *Estuaries*, *3*, 148–149.
- Dean, D. 1978a. Migration of the sandworm *Nereis virens* during winter nights. *Mar. Biol.*, *45*, 165–173.
- 1978b. The swimming of bloodworms (*Glycera* spp.) at night, with comments on other species. *Mar. Biol.*, *48*, 99–104.
- Desroy, N., F. Olivier and C. Retière. 1997. Effects of individual behaviour, inter-individual interactions with adult *Pectinaria koreni* and *Owenia fusiformis* (Annelida, Polychaeta), and hydrodynamism on *Pectinaria koreni* recruitment. *Bull. Mar. Sci.*, *60*, 547–558.
- Dobbs, F. C. and J. M. Vozarik. 1983. Immediate effects of a storm on coastal infauna. *Mar. Ecol. Prog. Ser.*, *11*, 273–279.
- Emerson, C. W. and J. Grant. 1991. The control of soft-shell clam (*Mya arenaria*) recruitment on intertidal sandflats by bedload sediment transport. *Limnol. Oceanogr.*, *36*, 1288–1300.
- Fauchald, K. and P. A. Jumars. 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanogr. Mar. Biol. Ann. Rev.*, *17*, 193–284.
- Forbes, T. L. and G. L. Lopez. 1990. The effect of food concentration, body size, and environmental oxygen tension on the growth of the deposit-feeding polychaete, *Capitella* species 1. *Limnol. Oceanogr.*, *35*, 1535–1544.
- Gallagher, E. D., P. A. Jumars and D. D. Trueblood. 1983. Facilitation of soft-bottom benthic succession by tube builders. *Ecology*, *64*, 1200–1216.
- Giangrande, A. 1997. Polychaete reproductive patterns, life cycles and life histories: an overview. *Oceanogr. Mar. Biol. Ann. Rev.*, *35*, 323–386.
- Gunther, C. 1992. Dispersal of intertidal invertebrates: a strategy to react to disturbances of different scales? *Neth. J. Sea Res.*, *30*, 45–56.
- Hentschel, B. T. 1999. Growth rates of interface-feeding benthos: effects of flow and the flux of nutritious components of natural sediments. Abstract, 1999 Aquatic Science Meeting, Santa Fe.
- Hunt, H. L. and L. S. Mullineaux. 2002. The roles of predation and postlarval transport in recruitment of the soft shell clam (*Mya arenaria*). *Limnol. Oceanogr.*, *47*, 151–164.
- Janssen-Stelder, B. 2000. The effect of different hydrodynamic conditions on the morphodynamics of a tidal mudflat in the Dutch Wadden Sea. *Cont. Shelf Res.*, *20*, 1461–1478.
- Le Hir, P., W. Roberts, O. Cazaillet, M. Christie, P. Bassoullet, and C. Bachor. 2000. Characterization of intertidal flat hydrodynamics. *Cont. Shelf Res.*, *20*, 1433–1459.
- Levin, L. A. 1984a. Life history and dispersal patterns in a dense infaunal polychaete assemblage: community structure and response to disturbance. *Ecology*, *65*, 1185–1200.
- 1984b. Multiple patterns of development in *Streblospio benedicti* Webster (Spionidae) from three coasts of North America. *Biol. Bull.*, *166*, 494–508.
- MacArthur, R. H. 1972. *Geographical Ecology: Patterns in the Distribution of Species*, Harper and Rowe Publishers, 259 pp.
- Mazurkiewicz, M. 1975. Larval development and habits of *Laeonereis culveri* (Webster) (Polychaeta: Nereidae). *Biol. Bull.*, *149*, 186–204.
- Norkko, A., V. J. Cummings, S. F. Thrush, J. E. Hewitt and T. M. Hume. 2001. Local dispersal of juvenile bivalves: implications for sandflat ecology. *Mar. Ecol. Prog. Ser.*, *212*, 131–144.

- Nowell, A. R. M., P. A. Jumars and J. E. Eckman. 1981. Effects of biological activity on the entrainment of marine sediments. *Mar. Geol.*, *42*, 133–153.
- Nowell, A. R. M., P. A. Jumars, R. F. L. Self and J. B. Southard. 1989. Effects of sediment transport and deposition on infauna: results obtained in a specially designed flume, in *Ecology of Marine Deposit Feeders*, G. Lopez, G. Taghon and J. Levinton, eds., Springer-Verlag, NY, 303–328.
- Olivier, F., N. Desroy and C. Retière. 1996a. Habitat selection and adult-recruit interactions in *Pectinaria koreni* (Malmgren) (Annelida: Polychaeta) post-larval populations: Results of flume experiments. *J. Sea Res.*, *36*, 217–226.
- Olivier, F., C. Vallet, J. Dauvin and C. Retière. 1996b. Drifting in post-larvae and juveniles in an *Abra alba* (Wood) community of the eastern part of the Bay of Seine (English Channel). *J. Exp. Mar. Biol. Ecol.*, *199*, 89–109.
- Palmer, M. A., J. D. Allan and C. A. Butman. 1996. Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. *Trends Ecol. & Evol.*, *11*, 322–326.
- Powers, S. P. and C. H. Peterson. 2000. Conditional density dependence: the flow trigger to expression of density-dependent emigration in bay scallops. *Limnol. Oceanogr.*, *45*, 727–732.
- Reed, D. J. 1988. Sediment dynamics and deposition in a retreating coastal salt marsh. *Estuar. Coast. Shelf Sci.*, *26*, 67–80.
- Rhoads, D. C., P. L. McCall and J. Y. Yingst. 1978. Disturbance and production on the estuarine seafloor. *Am. Sci.*, *66*, 577–586.
- Roman, C. T. 1984. Estimating water volume discharge through salt-marsh tidal channels; an aspect of material exchange. *Estuaries*, *7*, 259–264.
- Savidge, W. B. and G. L. Taghon. 1988. Passive and active components of colonization following two types of disturbance on intertidal sandflat. *J. Exp. Mar. Biol. Ecol.*, *115*, 137–155.
- Scheltema, R. S. 1986. On dispersal and planktonic larvae of benthic invertebrates: an eclectic overview and summary of problems. *Bull. Mar. Sci.*, *39*, 290–322.
- Shull, D. H. 1997. Mechanisms of infaunal polychaete dispersal and colonization in an intertidal sandflat. *J. Mar. Res.*, *55*, 153–179.
- Smith, C. R. and S. J. Brumsickle. 1989. The effects of patch size and substrate isolation on colonization modes in intertidal sediments. *Limnol. Oceanogr.*, *34*, 1263–1277.
- Stocks, K. 2000. Factors Influencing Macroinfaunal Community Structure in Saltmarshes. Ph.D. Dissertation, Rutgers University, 180 pp.
- . 2001. Effects of microalgae and food limitation on the recolonization of benthic macrofauna into *in situ* saltmarsh-pond mesocosms. *Mar. Ecol. Prog. Ser.*, *221*, 93–104.
- Suk, N. S., Q. Guo, and N. P. Psuty. 1999. Suspended solids flux between salt marsh and adjacent bay: a long-term continuous measurement. *Estuar. Coast. Shelf Sci.*, *49*, 61–81.
- Thiébaud, E., J. Dauvin and Z. Wang. 1996. Tidal transport of *Pectinaria koreni* postlarvae (Annelida: Polychaeta) in the Bay of Seine (eastern English Channel). *Mar. Ecol. Prog. Ser.*, *138*, 63–70.
- Thiébaud, E., Y. Lagaduec, F. Olivier, J. C. Dauvin and C. Retière. 1998. Do hydrodynamic factors affect the recruitment of marine invertebrates in a macrotidal area? *Hydrobiologia*, *375/376*, 165–176.
- Thrush, S. F., R. D. Pridmore, J. E. Hewitt and V. J. Cummings. 1992. Adult infauna as facilitators of colonization on intertidal sandflats. *J. Exp. Mar. Biol. Ecol.*, *159*, 253–265.
- Turner, S. J., J. Grant, R. D. Pridmore, J. E. Hewitt, M. R. Wilkinson, T. M. Hume and D. J. Morrissey. 1997. Bedload and water-column transport and colonization processes by post-settlement benthic macrofauna: Does infaunal density matter? *J. Exp. Mar. Biol. Ecol.*, *216*, 51–75.
- Uncles, R. J. and J. A. Stephens. 2000. Observations of currents, salinity, turbidity and intertidal mudflat characteristics and properties in the Tavy Estuary, UK. *Cont. Shelf Res.*, *20*, 1531–1549.

- Underwood, A. J. and P. G. Fairweather. 1989. Supply-side ecology and benthic marine assemblages. *Trends Ecol. & Evol.*, *4*, 16–20.
- Whitlatch, R. B., A. M. Lohrer, S. F. Thrush, R. D. Pridmore, J. E. Hewett, V. J. Cummings and R. N. Zajac. 1998. Scale-dependent benthic recolonization dynamics: life stage-based dispersal and demographic consequences. *Hydrobiologia*, *375/376*, 217–226.
- Whitlatch, R. B. and R. W. Osman. 1998. A new device for studying benthic invertebrate recruitment. *Limnol. Oceanogr.*, *43*, 516–523.
- Wilson, W. H., Jr. 1983. The role of density dependence in a marine infaunal community. *Ecology*, *64*, 295–306.
- 1994. Dispersal of soft-bottom benthos: migration through the water column or through the sediment? *in* *Reproduction and Development of Marine Invertebrates*, H. W. Wilson, Jr., S. A. Stricker and G. L. Shinn eds., John Hopkins University Press, Baltimore, MD, 303–312.
- Woodin, S. A., S. M. Lindsay and D. S. Wethey. 1995. Process-specific recruitment cues in marine sedimentary systems. *Biol. Bull.*, *189*, 49–58.

Received: 9 May 2002; revised: 4 November, 2002.