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Active habitat selection by *Capitella* sp. I larvae. I. Two-choice experiments in still water and flume flows

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ABSTRACT

Sediment selection by settling larvae of the opportunistic polychaete *Capitella* sp. I was determined in laboratory still-water and flume experiments, where larvae were given a choice between two highly contrasting sediment treatments. In most cases, 2-h experiments were conducted with a natural, organic-rich mud and an abiotic, glass-bead mixture with a grain-size distribution similar to the mud, as the sediment treatments. Spatial settlement patterns were also determined in sediment arrays containing mud only. Two types of flume flows were tested, both with a near-surface velocity of ~ 5 cm s^{-1}, but one flow was cyclical, varying between about 2 and 7 cm s^{-1} with a period of 6.3 min, and one was steady with a boundary shear velocity of 0.26 cm s^{-1}. Plastic spheres were added to the experiments as passive larval mimics. *Capitella* sp. I larvae selected the muddy sediment as opposed to the glass beads in all experiments conducted, consistent with food requirements of the deposit-feeding adults and with field distributions. Selectivity was insensitive to a range of experimental conditions, including flow, water temperature, light regime, experimental duration, distance sediment treatments were separated, time of year and larval batch. Experiments furthermore suggested that contact with the sediment is required to elicit a settlement response. Flows tested were weak compared to the range likely encountered by larvae of this species, even in depositional areas in the field; however, horizontal flow speeds within larval search distances of the bottom exceeded horizontal swim speeds of the larvae (determined in still water). A model for sediment selection in the field is proposed where larvae move up and down close to the bottom, while being transported by the flow, and test sediments on contact. Selection is thus accomplished by active acceptance or rejection of touchdown sites. This model was qualitatively supported by observations of larvae in still water and manipulative flume experiments. These results suggest that active sediment selection may be responsible, at least in part, for field distributions of this species.

1. Introduction

Settlement of planktonic larvae of benthic invertebrates is undoubtedly determined by a combination of active larval behaviors (in response to biological, chemical

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and physical factors) and hydrodynamical processes that distribute larvae as if they were passive particles (e.g., Scheltema, 1986; Butman, 1987; Woodin, 1991). The spatial and temporal scales over which active biological versus passive physical processes primarily determine species distributions likely depends on the behaviors and life-history characteristics of the organism and the nature of flows within its dispersal ambit (Grassle *et al.,* 1992b). Defining the relative importance of active versus passive processes during larval settlement is critical to evaluating the role of the larval stage in determining life history traits and species distributions.

This paper presents laboratory experiments on the habitat-selection capabilities of larvae of the infaunal polychaete *Capitella* sp. I (Grassle and Grassle, 1976) in still water and moderately slow, turbulent, flume flows. Results of four of our earliest experiments (Expts. 3, 11, 12, 13; Table 1) were briefly described in Butman *et al.* (1988b). Because most of the evidence for active selection by infaunal invertebrates has been derived from small-scale (of order millimeters to centimeters), still-water, laboratory experiments (Butman, 1987), our study focused on the first-order questions: 1) can larvae that are clearly selective in still water execute this choice in turbulent flow and, 2) if so, how might this be accomplished? To address these questions simple, two-choice experiments using highly contrasting (in terms of organic content) sediment treatments were performed in still water and flume flows. A subsequent study addresses selection among several natural sediments that might be encountered by larvae in the field, explores aspects of the sediments to which the larvae may respond, and evaluates settlement and selectivity in relatively fast versus slow flume flows and as a function of larval age (Grassle *et al.,* 1992a).

Capitella sp. I is a member of the *Capitella* sibling-species complex (Grassle and Grassle, 1976, 1978; Grassle, 1980). All species are subsurface deposit feeders that commonly occur in disturbed, organic-rich, muddy habitats (e.g., Grassle and Grassle, 1978; Sanders *et al.,* 1980). They can be identified unequivocally using allozyme electrophoresis (Grassle and Grassle, 1976; Grassle, unpublished) and karyotypes (Grassle *et al.,* 1987). Egg size and larval development mode (Grassle and Grassle, 1976), mature sperm morphology, genital spine number and morphology in males and hermaphrodites, and external larval ciliary banding patterns (Eckelbarger and Grassle, 1987) are also useful in distinguishing among some species.

Capitella sp. I was chosen for this study for both ecological and evolutionary reasons. Of all the *Capitella* species studied to date, *Capitella* sp. I is the most opportunistic, has the most widespread geographic distribution and, on a local scale, is the most ubiquitous spatially and temporally. Its opportunistic life history characteristics, which are shared by all of the sibling species, include iteroparity and brooding of developing embryos in the parent's tube. *Capitella* sp. I also has one of the shortest generation times (70–80 days at 15°C, 35–40 days at 20°C, Grassle and Grassle, 1976, Grassle, unpublished; 4 weeks at 15–20°C, Tsutsumi *et al.,* 1990) and the lecithotrophic metatrochophores that hatch from the parental tube are compe-

tent to settle when offered an appropriate sediment cue (Dubilier, 1988; Grassle, unpublished). Reproductive output is also known to vary in response to both the quality and quantity of food (Grémare *et al.,* 1988). All of these characteristics contribute to the rapid population increases and high local densities seen under a variety of disturbed, organic-enriched conditions in the field (e.g., Grassle and Grassle, 1974; Grassle and Grassle, 1976; Tsutsumi, 1987, 1990; Grassle, unpublished), and to cyclical changes in population density observed in laboratory microcosms (Chesney and Tenore, 1985; Grémare *et al.,* 1989a,b).

The *Capitella* sibling species are also of interest from an evolutionary perspective because it is common to find sibling species with either direct development, lecithotrophic larvae or planktotrophic larvae occurring sympatrically (Grassle and Grassle, 1974, 1978; Grassle and Grassle, 1976; Grassle, 1980). These same species, however, show predictable differences in their spatial and temporal distributions. The phenomenon of related species within a single genus displaying a variety of developmental modes occurs in many phyla, and has led to speculation that a change in development mode is a key step in speciation (Thorson, 1950; Mileikovsky, 1971; Vance, 1973; Strathmann, 1978; Caswell, 1981; Hoagland, 1984; Raff, 1987), and that the primitive condition involves a planktotrophic mode of development (Jägersten, 1972). One might speculate that for species within a sibling species complex such as *Capitella,* the shifting balance between the adaptive value of local population increases and the advantages of mechanisms facilitating the location of new habitats will result in differential selection for particular larval characteristics in the various species.

The ways in which the lecithotrophic larvae of *Capitella* sp. I disperse away from the parental population and how they find and colonize newly-disturbed habitats are poorly understood. Recent work has shown that, although the larvae are competent and responsive to sediment cues at hatching, they can also delay settlement for up to five days without significant mortality (Grassle, unpublished) or subsequent negative effects on growth and fecundity (Pechenik and Cerulli, 1991). The larvae, therefore, have the potential for dispersal and observed distributions of adults may result either from indiscriminate larval settlement followed by differential survival in organic-rich versus food-poor environments or from active habitat location and discriminate settlement. Determining the likelihood of these alternative mechanisms for establishing adult populations was the major motivation for this research.

2. Materials and methods

a. Larval cultures. Brood tubes with developing embryos were taken from cultures of *Capitella* sp. I adults using stocks from various geographical locations along the west and east coast of the United States. Care was taken to ensure that matings produced outcrossed larvae. All adult culture and larval handling techniques were similar to those previously described for this species (Grassle and Grassle, 1976; Butman *et al.,* 1988a). Cultures were maintained at 15°C and isolated brood tubes were examined

daily for spontaneous larval hatching. To obtain sufficient larvae for a sediment-selection experiment and concurrent competency tests conducted on a given day, swimming larvae were pooled from up to 20 broods that had hatched within 48 h prior to the experiment. Larvae that hatched more than a few hours prior to an experiment were held in filtered seawater at 15°C without any settlement cues and examined just before being pooled with other larvae. If any individuals within a brood showed signs of spontaneous settlement and metamorphosis, the entire brood was rejected. The pooled larvae were gradually brought to the experimental temperature (Table 1) on the morning of the experiment.

b. Flume and still-water box for sediment-selection experiments. Sediment-selection experiments in moving water were conducted in the "Paddle-Wheel Flume" (Fig. 1) located in the Coastal Research Laboratory at Woods Hole Oceanographic Institution. This is a recirculating, racetrack-design, seawater flume constructed of plexiglas. The outer dimensions of the racetrack are 2.0 m (maximum width) and 8.5 m (maximum length) and the channel is 50 cm wide by 30 cm deep, except at the paddle wheel location. The flow is driven by a paddle wheel in a counter-clockwise direction. The 2-m-diameter paddle wheel consists of eight freely articulating, plexiglass paddles (76.2 m long × 54.6 cm wide × 1.3 cm thick) that swing on rods and are adjusted to hang vertical during all phrases of the rotation. At the bottom of their descent, the paddles come within a centimeter of the flume bottom. Initially (Expts. 6, 9–13 and 17–19; Table 1) flow straighteners, to limit cross-stream circulation around the bend (discussed later), were installed only in the upstream bend of the channel. Because of evidence for significant cross-stream redistribution of larvae (see Results), however, flow straighteners were eventually installed also in the downstream bend prior to Expts. 5, 7, 8 and 14–16 (Table 1).

The flume was originally built with a 10-cm-deep false bottom in the 6.1-m-long straightaway on the side opposite the paddle wheel. The false bottom consisted of four sections that fit snugly end-to-end to make a smooth transition in bottom surface texture. Rubber tubing was squeezed between the false bottom and flume walls to limit water circulation below the false bottom. The third section of the false bottom, located 4.5 m from the bend, was 50 cm square and contained the sediment array (described later) for Expts. 6, 7, 9–13, and 15–19 (Table 1). The sediment array was placed as far downstream from the bend as possible to permit maximum boundary-layer growth (e.g., see Nowell and Jumars, 1987). For logistical reasons (i.e., ease of cleaning and of insertion and removal of the sediment array), the flume straightaway was remodeled during the summer of 1989. The false bottom was removed and a section of the flume bottom was then modified to contain the sediment array, again located 4.5 m from the bend and flush with the surrounding flume bottom. Flume Expts. 8 and 14 (Table 1) were conducted in and still-water Expts. 1 and 2 (Table 1)

were conducted on top of the remodeled flume. Flow characteristics were unchanged by the remodeling.

The flume is located in a high bay that is not well-controlled for temperature and has diffuse overhead lighting. Prior to remodeling, the flume was oriented such that the only wall in the high bay that contained shaded windows was parallel to the straightaway containing the sediment array, creating the potential for a cross-stream gradient in natural light intensity (evaluated and discussed later). The remodeled flume was rotated 90° so that the windows faced the downstream bend.

All flume experiments, except Expts. 9 and 10 (Table 1), were conducted in a moderately slow (~ 5 cm s^{-1} at 7 cm above the bottom), turbulent flow with a bottom shear velocity (u_*) of 0.26 cm s^{-1} (see Appendix). A series of vertical profiles of mean horizontal velocities confirm that, at this speed, the array was positioned at a downstream location and within the central region of flow that was fully developed and essentially one-dimensional (see Appendix). This flow was chosen to be within the range of flows typical of coastal embayments where *Capitella* sp. I populations can be abundant, such as Buzzards Bay, Massachusetts. Vertical profiles of mean velocity for tidally driven flows in Buzzards Bay were constructed, based on field measurements at "Station 35" (14 m depth; described in Sanders *et al.,* 1980; Butman, 1989) and bottom boundary-layer theory, by Butman (1986) and indicate a maximum u_* of ~ 0.6 cm s^{-1} at peak flood or ebb tide. The u_* of the flume flow was thus near the midpoint of the range of these tidal flows, which drop to zero at slack tide.

Flow Expts. 9 and 10 (Table 1) were the first experiments conducted in the Paddle-Wheel Flume and, because of an initial design problem, the flow was cyclical. During these experiments, flow speed was measured every 10 s for 10 min intervals using a Marsh-McBirney electromagnetic current meter mounted 7 cm above the bottom downstream of the array. The mean flow speed was ~ 5 cm s^{-1}, but speeds gradually varied between 2 and 7 cm s^{-1} (Fig. 2) over a period of 6.3 min, which was the period for one paddle-wheel revolution in these experiments. This problem was remedied by modifications to the motor driving the paddle wheel, resulting in a steady mean flow (Fig. 2 and Appendix) for all other flume experiments. The cyclical flow in Expts. 9 and 10 does not mimic a specific natural flow in the field; however, settlement in this flow provides an interesting contrast to the steady flow and still-water cases and may give additional insight regarding larval settlement-flow interactions. Boundary shear velocities cannot be calculated for this cyclical flow because it violates the assumption of an equilibrium boundary layer (i.e., where temporal and spatial gradients are small).

The still-water, sediment-selection experiments were conducted in a 50-cm-square by 30-cm-deep plexiglass box. The sediment array was placed inside the box. During experiments, the still-water box was placed on top of the flume raceway, slightly downstream of the array, so that larvae settling in still water would be exposed to

Table 1. Conditions for sediment-selection experiments

Experiment	Date	Type of flow	Flume orientation[α]	Seawater temperature (°C)	Time larvae added (h:min)	Mean sphere diameter (μm)	Addition method for flume[β]	Sediment treatments	Treatment design	Type of array
Still-Water Experiments										
1	9-12-89	Still	Perpendicular	24.4	10:07	383		NBH Mud	All mud	4 × 4
2	10-2-89	Still	Perpendicular	20.5	10:15	383		NBH Mud	All mud	5 × 5
3	2-9-87	Still	Parallel	16.2	12:45	none		NBH Mud Glass Beads	Checkerboard	5 × 5
4	11-19-87	Still	Parallel	21.6	09:50	383		NBH Mud Beads on Mud	Checkerboard	5 × 5
Flow Experiments										
5	8-12-87	Steady	Parallel	21.2	09:00	none	2	NBH Mud	Strips around flume[δ]	none
6	7-22-87	Steady	Parallel	22.2	09:50	383	2	NBH Mud	All mud	5 × 5
7	9-3-87	Steady	Parallel	21.8	09:50	383	2	NBH Mud	All mud	5 × 5
8	9-18-89	Steady	Perpendicular	20.9	10:05	383	5	NBH Mud	All mud	4 × 4
9	2-23-87	Cyclical	Parallel	16.1	13:00	200	1	NBH Mud Glass Beads	Checkerboard	5 × 5
10	3-17-87	Cyclical	Parallel	15.5	21:30[ε]	200	1	NBH Mud Glass Beads	Checkerboard	5 × 5
11	4-22-87	Steady	Parallel	17.5	13:45	200	2	NBH Mud Glass Beads	Checkerboard	5 × 5
12	6-24-87	Steady	Parallel	20.5	01:30[γ]	280	2,4	NBH Mud Glass Beads	Checkerboard	5 × 5
13	7-15-87	Steady	Parallel	22.8	10:30	383	2	NBH Mud Glass Beads	Checkerboard	5 × 5

Table 1. (Continued)

Experiment	Date	Type of flow	Flume orientation[α]	Seawater temperature (°C)	Time larvae added (h:min)	Mean sphere diameter (μm)	Addition method for flume[β]	Sediment treatments	Treatment design	Type of array
14	9-25-89	Steady	Perpendicular	19.1	11:00	383	5	NBH Mud Glass Beads	Checkerboard	4 × 4
15	9-25-87	Steady	Parallel	19.2	11:10	383	2	NBH Mud Barite on Mud	Checkerboard	5 × 5
16	10-7-87	Steady	Parallel	19.6	10:40	383	2	NBH Mud Beads on Mud	Checkerboard	5 × 5
17	5-7-87	Steady	Parallel	16.3	11:23	200	2,3	NBH Mud Glass Beads	Alternating strips in columns	5 × 5
18	5-14-87	Steady	Parallel	17.4	11:00	200	2,3	NBH Mud Glass Beads	Alternating strips in rows[λ]	5 × 5
19	5-27-87	Steady	Parallel	18.4	10:07	200	2	NBH Mud Glass Beads	Alternating strips in rows[μ]	5 × 5

[α]Perpendicular = perpendicular to windows in the high bay; Parallel = parallel to windows in the high bay (see text).
[β]Numbers refer to addition methods described in text. Where two numbers are listed, the first refers to addition method for larvae and the second to addition method for spheres.
[δ]4-cm-wide strips placed cross-stream at five locations around flume (see text).
[ε]Experiment duration of 12 h.
[γ]Experiment conducted completely in dark—on a moonless night with all room lights switched off.
[λ]NBH Mud row at leading edge.
[μ]Glass Beads row at leading edge.

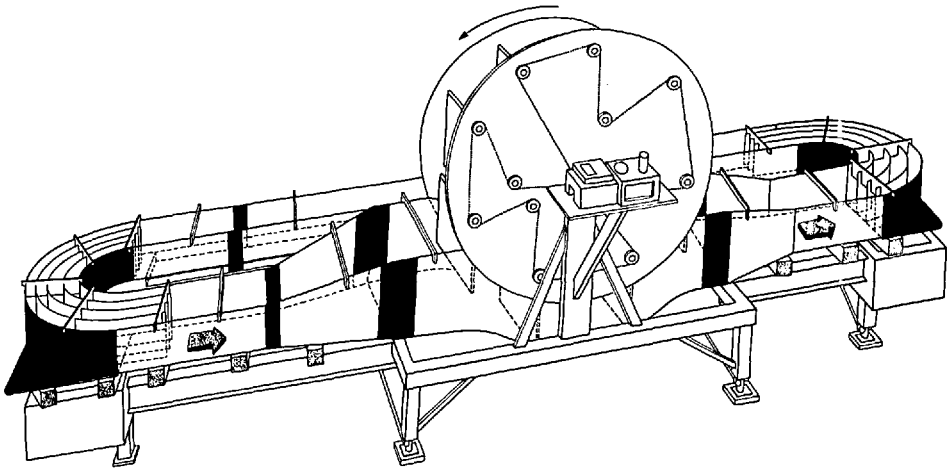


Figure 1. Perspective view of the Paddle-Wheel Flume (paddle wheel is actually equidistant from the bends). Broad arrows indicate direction of flow and the thin arrow indicates direction of paddle-wheel rotation. Experiments were conducted in the straightaway on the side opposite the paddle wheel.

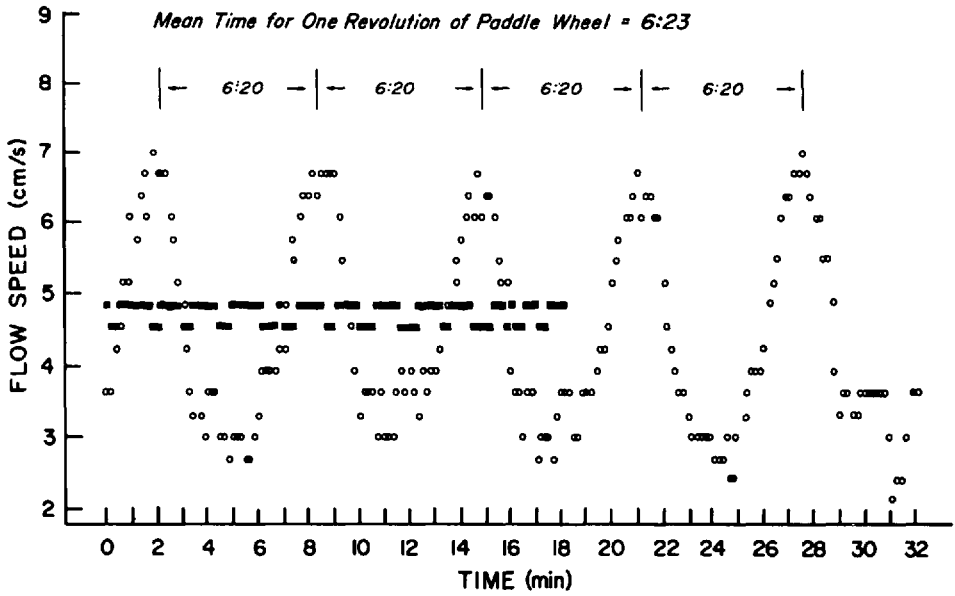


Figure 2. Records of flow speed in the Paddle-Wheel Flume before (open circles) and after (closed squares) the cyclical flow problem was remedied (see text). Measurements were taken every 10 s using a Marsh-McBirney electromagnetic current meter mounted 7 cm above the bottom downstream from the sediment array. The approximate period of the flow cycle is given above the graph. The cyclical record is typical of flow conditions during Expts. 9 and 10, and the steady record is typical of all other flume experiments.

approximately the same light and temperature regime as larvae settling in the flume sediment array.

The flume and still-water box were filled to 10 cm depth with 1-μm-filtered seawater which was allowed to equilibrate to room temperature prior to the experiments. This temperature varied, however, between 16.1 and 24.4°C depending on the time of year when experiments were conducted (Table 1). In an attempt to control for natural light (from the windows) between experiments, all experiments, except Expts. 10 and 12, were conducted at approximately the same time of day (Table 1). Experiment 10 was conducted for 12 h (Table 1) to determine if a longer experimental duration affected larval settlement and selectivity; it ran from 21:30–09:30. Experiment 12 was conducted completely in the dark, on a moonless night, to determine if light was required for larval sediment selection, particularly given that the NBH Mud is dark brown in color and the Glass Beads are white. Variation in light energy across the 50-cm square region containing the sediment array in the flume and the still-water box was measured one cloudy (30 March 1989) and one sunny (12 April 1989) day using an International Light 700 Research Radiometer (Model SEE-010 2π, cosine-corrected detector), with spectral sensitivity for indoor visible and infrared light. The detector, with its 2.5-cm-diameter sensor facing up, was placed in the corners and midway along each of the sides of the still-water box and at equivalent locations in the flume.

c. Sediment array and treatments. For all experiments, except Expts. 1, 5, 8 and 14 (Table 1), one or two sediment treatments were arranged in a five-by-five array of 4 × 4 × 1-cm deep compartments (separated by 3 mm partitions) milled out of the central region of a 50-cm square plexiglass plate. This plate served as the third section of the flume false bottom. The compartments were filled with sediment until the sediment was flush with the surrounding plate. The filled compartments were covered with a tight-fitting lid (shown in Bachelet *et al.,* 1992) during installation and removal from the still-water box and flume to minimize disturbance to the sediment surface. The underside of the lid contained 25 shallow recesses with 2-mm-thick dividers that met precisely with the compartments in the array to prevent contamination between adjacent compartments. For Expts. 1, 8 and 14, sediments were placed in a four-by-four array of 4.5-cm-diameter by 1-cm-deep cylindrical compartments (separated by a minimum of 10.5 mm) milled out of a plexiglass plate that was installed in the bottom of the remodeled flume. The sediment area per compartment ($\sim$16 cm^2) and the total area of flume bottom covered by the array compartments ($\sim$400 cm^2) was similar in the two arrays. In the four-by-four array, however, compartments were separated by a larger expanse of plexiglass plate than in the five-by-five array. For Expt. 5, strips of NBH Mud (4 cm wide by 1.0–1.5 mm deep) were placed cross-stream (to within a centimeter of the wall) directly on the flume

bottom or false bottom before and after the bends and at the leading edge of the array.

Sediment treatments were selected based on known larval preferences (e.g., Dubilier, 1988; Grassle, unpublished) and adult distributions (e.g., Grassle and Grassle, 1978; Sanders *et al.,* 1980). Two highly contrasting sediment treatments were selected to elicit a clear settlement response in still water. An organic-rich, muddy sediment (typical percentages of organic carbon, hydrogen and nitrogen (C:H:N) of 3.19:0.63:0.32 and 76.1% of particles <63 μm; see Bachelet *et al.,* 1992) collected from 10-m depth in outer New Bedford Harbor, Massachusetts (top 2–3 cm; Van Veen grabs), hereafter called "NBH Mud," was expected to be highly attractive to settling larvae of *Capitella* sp. I. An abiotic, low-organic (typical C:H:N of 0.1:0.1:0; see Bachelet *et al.,* 1992), glass-bead mixture (Ferro Class IVA Microbeads, particle density = 2.42 g cm^{-3}; mixture of 40% 13–44 μm, 30% 53–74 μm and 30% 88–125 μm particles), hereafter called "Glass Beads," with a grain-size distribution roughly similar to the NBH Mud (i.e., 70.0% of Glass Beads were <63 μm), was expected to be unattractive to settling larvae. For Expt. 15, the mineral barite, hereafter called "Barite," in the form of barium sulfate (American Petroleum Institute "Lab-Standard Barite"), was used as the abiotic, low-organic sediment expected to be unattractive compared to NBH Mud. Barite is similar to Glass Beads in its low organic carbon content (C:H:N of 0.03:0.04:0; see Bachelet *et al.,* 1992), but has a higher percentage of fine particles (97.5% of particles <63 μm, according to the factory). Barite was selected as an additional abiotic, low-organic treatment and also because it is an exotic particle introduced into the marine environment, sometimes in large quantities, during exploratory and production drilling activities (e.g., Boesch and Rabalais, 1987). These settlement experiments were part of a larger study to assess the effects of drilling discharges on benthic communities (e.g., Hyland *et al.,* 1990).

NBH Mud was pushed through a 1-mm sieve to remove large pieces of shell, rock or debris that would contribute significant bed roughness, as flume experiments were designed for a hydrodynamically smooth-bed flow (see Appendix). The mud was frozen and thawed prior to use. Glass Beads were mixed, thoroughly washed in filtered seawater, frozen and thawed prior to use. Barite was mixed with filtered seawater prior to use. Arrangement of the treatments within the arrays is described later for each of the hypotheses tested.

d. Experimental procedures. To permit meaningful comparisons between selection experiments conducted on different days, we eventually developed standard procedures for conducting experiments, but initially this was an iterative process. That is, some aspects of the experiments could be standardized immediately (e.g., the schedule for filling the arrays and flume), but others (e.g., the method for adding larvae and spheres to the water) were modified to reduce between-experiment

variability. In addition, because temperature, light and larval batch varied between experiments, none of the experiments were replicated in all respects. Instead, we conducted repeated tests of settlement in one- or two-choice arrays under varying conditions (of light, temperature, larval brood, larval addition technique, etc.) that, in the end, did not appear to qualitatively affect sediment selectivity in this species.

Within 36 h of a selection experiment, sediments were thawed and ~12 h later the array was filled with sediments, the flume or still-water box was filled with 1-μm-filtered seawater, and the array was placed in the flume or still-water box. The lid on the array was carefully removed so the sediments were exposed to seawater. Seawater and sediments thus equilibrated to ambient air temperature for about 16 h prior to an experiment.

In all experiments but one (Expt. 14), 1200 larvae were added, resulting in concentrations of ~48 larvae liter^{-1} in the still-water box (~25 liter volume) and ~1.2 larvae liter^{-1} in the flume (~1000 liter volume), assuming larvae were uniformly distributed. In Expt. 14, 3600 larvae were added to the flume. In addition, 1200 polystyrene spheres (Duke Scientific, DVB Microspheres; 1.05 g cm^{-3} density according to factory specifications) were added in all flume experiments except two (Expts. 5 and 9, where no spheres and 1800 spheres were added, respectively) and in all still-water experiments except one (Expt. 3, where no spheres were added). Spheres served as passive larval mimics and were also used for evaluating the extent to which our addition techniques may have uniformly distributed the larvae (see below). Three sphere sizes, 200 ± 12, 270 ± 15 and 383 ± 8 μm diameter (according to factory specifications), with mean Stokes' fall velocities of 0.06, 0.11 and 0.22 cm s^{-1} (30 ppt, 20°C seawater), were used in different experiments (Table 1). Mean (± 1 S.D.) gravitational fall velocities of anesthetized, one-day-old, *Capitella* sp. I larvae were 0.09 ± 0.009 cm s^{-1} for "Brood A" and 0.08 ± 0.008 cm s^{-1} for "Brood B" (N = 3 replicate dishes per brood, the dishes containing about 50 larvae each; Butman *et al.*, 1988a). The two smallest bead sizes thus represent non-swimming larvae passively sinking toward the bottom. In still water and in the flume, however, *Capitella* sp. I larvae were always observed swimming down (not passively sinking) to the bottom, so the largest bead size was chosen to mimic downward swimming. A vertical swim speed of 0.2 cm s^{-1} is at the high end of the range measured for *Capitella* sp. I larvae (Butman, unpublished, using methods similar to Butman *et al.*, 1988a).

Developing easy and reliable techniques for unbiased introductions of larvae and spheres into the flume and still-water box was an ongoing process. The goals were to: 1) maximize contact with the array on the first transit downstream in the flume and on direct free-fall to the bottom in the still-water box, 2) impart minimal momentum to the larvae and particles and 3) impart minimal disturbance to the water column. In the still-water box, larvae and spheres initially (Expts. 3 and 4) were mixed with seawater and added, separately, using a plastic spoon immersed ~1 cm below the

water surface and drawn in sweep patterns designed to uniformly distribute them in the water above the array. This was a cumbersome and time-consuming technique, however, and eventually (Expts. 1 and 2) larvae and spheres were added together in 16 aliquots poured down the side of a funnel which had its stem immersed just below the water surface above each compartment in the array (see Grassle *et al.,* 1992a). The order of addition to the compartments was randomized for each experiment.

In the flume, larvae and spheres were introduced upstream of the sediment array to maximize the probability that they would encounter the array on their first transit downstream. Upstream addition points were determined based on theoretical (Stokes') fall velocities of the spheres and on passive sinking rates and downward swim speeds of the larvae (Butman *et al.,* 1988a; Butman, unpublished). After trying several addition locations, the maximal recovery of larvae in the array resulted when they were added at upstream locations corresponding to a range of sinking rates between about 0.10 and 0.15 cm s^{-1} which, at the high end, exceeded their passive sinking rates (Butman *et al.,* 1988a), but were within the range of their downward swim speeds (Butman, unpublished). The consistent, very low numbers of spheres collected in the array (Table 2) was troublesome because the percentage of spheres recovered was usually too low for meaningful statistical analyses. We tried upstream addition points based on the still-water fall velocity of the mean sphere diameter only, on fall velocities of the mean and standard deviation of sphere diameter, and on other extremes. Eventually, to save time, we simply added the spheres with the larvae, and because sphere recovery was not substantially different, this practice was continued.

Larvae were added to the flume using three different addition techniques; these three methods plus two additional techniques were used for adding spheres to the flume. The five techniques are described below and the specific experiments for which a given technique was used are indicated in Table 1. 1) Initially, larvae and spheres were introduced into the flume with a plastic spoon, as in the still-water box. The spoon was swept across the central ~20 cm of the flume. 2) Next, larvae and spheres were mixed, separately, with seawater in 200 ml beakers that were gently tipped into the flow just below the water surface and swept across the central ~20 cm of the flume. 3) In two experiments, spheres were added to a tube (2.5 cm inside diameter, 14 cm long) filled with seawater, held parallel to the flow in the center of the channel and quickly uncapped at both ends. Spheres were coming out so slowly in Expt. 19, however, that eventually they were added to a 118 ml jar that was uncapped while the mouth pointed upstream. 4) Another sphere addition technique involved five parallel tubes (3.6 cm inside diameter, 8.3 cm long) held in a rack so that there was ~1 cm separating adjacent tubes. The tubes thus spanned the cross-stream distance of the array. The tubes were submerged just below the water surface and were quickly uncapped at both ends. 5) Finally, a "larval (and sphere) adder" was developed that incorporated the positive aspects of all other methods.

Table 2. Results of sediment-selection experiments.

Experiment	Sediment treatment	Number larvae $\bar{x} \pm$ 1SD (*N*)	Significance[a] of treatment effect	Total larvae in array (%)	Number spheres $\bar{x} \pm$ 1SD (*N*)	Significance[a] of treatment effect	Total spheres in array (%)
Still-Water Experiments							
1	NBH Mud	48.6 ± 11.5 (16)	NA	778 (64.8)	8.3 ± 5.2 (16)	NA	133 (11.1)
2	NBH Mud	36.7 ± 8.8 (25)	NA	918 (76.5)	15.8 ± 10.0 (25)	NA	395 (32.9)
3	NBH Mud	58.4 ± 9.9 (13)	***	774 (64.5)		no spheres added	
	Glass Beads	1.2 ± 1.7 (12)					
4	NBH Mud	49.4 ± 17.3 (13)	***	733 (61.1)	25.0 ± 11.1 (13)	NS	736 (61.3)
	Beads on Mud	7.6 ± 4.5 (12)			34.2 ± 15.3 (12)		
Flow Experiments							
5	NBH Mud	25.8 ± 7.9 (5)	NA	129 (10.8)		no spheres added	
6	NBH Mud	11.8 ± 9.1 (25)	NA	294 (24.5)	2.1 ± 2.2 (25)	NA	53 (4.4)
7	NBH Mud	12.0 ± 9.1 (25)	NA	300 (25.0)	0.7 ± 0.9 (25)	NA	17 (1.4)
8	NBH Mud	14.5 ± 6.7 (16)	NA	232 (19.3)	0.6 ± 0.5 (16)	NA	9 (0.8)
9	NBH Mud	5.7 ± 3.4 (13)	***	81 (6.8)	1.2 ± 1.2 (13)	NP	28[β] (1.6)
	Glass Beads	0.6 ± 0.7 (12)			1.0 ± 1.2 (12)		
10	NBH Mud	7.7 ± 4.0 (13)	***	103 (8.6)	0.3 ± 0.6 (13)	NP	13 (1.1)
	Glass Beads	0.2 ± 0.4 (12)			0.8 ± 1.2 (12)		
11	NBH Mud	17.3 ± 9.8 (13)	***	291 (24.2)	1.4 ± 2.1 (13)	NP	35 (2.9)
	Glass Beads	5.5 ± 4.3 (12)			1.4 ± 1.1 (12)		
12	NBH Mud	16.7 ± 14.3 (13)	***	221 (18.4)	0.5 ± 1.1 (13)	NP	13 (1.1)
	Glass Beads	0.3 ± 0.5 (12)			0.5 ± 0.7 (12)		
13	NBH Mud	16.2 ± 7.1 (13)	***	217 (18.1)	1.0 ± 1.4 (13)	NP	33 (2.8)
	Glass Beads	0.6 ± 1.2 (12)			1.6 ± 1.4 (12)		
14	NBH Mud	40.6 ± 23.9 (8)	***	334[δ] (9.3)	1.2 ± 1.0 (8)	NP	20 (1.7)
	Glass Beads	1.1 ± 1.2 (8)			1.2 ± 1.0 (8)		
15	NBH Mud	15.3 ± 8.5 (13)	*	319 (26.6)	0.3 ± 0.6 (13)	NP	10 (0.8)
	Barite on Mud	10.0 ± 3.1 (12)			0.5 ± 0.7 (12)		
16	NBH Mud	9.3 ± 6.3 (13)	***	124 (10.3)	10.3 ± 13.1 (13)	NS	280 (23.3)
	Beads on Mud	0.2 ± 0.4 (12)			12.2 ± 16.7 (12)		
17	NBH Mud	5.7 ± 2.9 (15)	NA	88 (7.3)	0.2 ± 0.4 (15)	NA	6 (0.5)
	Glass Beads	0.2 ± 0.4 (10)			0.3 ± 0.7 (10)		
18	NBH Mud	6.7 ± 4.5 (15)	NA	113 (9.4)	0 (15)	NA	4 (0.3)
	Glass Beads	1.2 ± 1.4 (10)			0.4 ± 1.3 (10)		
19	NBH Mud	6.9 ± 5.0 (10)	NA	81 (6.8)	0 (10)	NA	4 (0.3)
	Glass Beads	0.8 ± 1.1 (15)			0.3 ± 0.5 (15)		

[a]See Tables 3 and 6. *$p \leq 0.05$; **$p \leq 0.01$; ***$p \leq 0.001$; NA = not applicable; NP = Statistics not performed because sphere settlement was <3%; NS = not significant at $p \leq 0.05$.

[β]1800 spheres added.

[δ]3600 larvae added.

This consisted of a rectangular box that was placed cross-stream and spanned the central 20 cm of the flume. The bottom of the box, which pointed into and away from the flow, was machined to a thin beveled edge and the long sides of the rectangle were drawn up vertically so the contents (larvae and spheres mixed together in seawater) were washed out of the box and downstream by the flow.

All still-water and flow experiments except one were run for 2 h; Expt. 10 ran for 12 h. At the end of the still-water and flume experiments, the lid was installed on the sediment array. The lid was positioned above the array by sliding it down four temporary "guide rods" screwed into the four corners of the array; this permitted installation of the lid with virtually no disturbance to sediments in the compartments. After the lid was installed, flow was stopped in the flume. Water to within ~1 cm above the array was drained before the array was removed from the flume and still-water box. Sediment in each compartment of the array was removed and the samples sorted live for metamorphosed (i.e., loss of all larval ciliation) *Capitella* sp. I juveniles and for spheres.

e. Competency tests. During each sediment-selection experiment, still-water tests of the competency of the experimental animals to settle, metamorphose and survive for several days were conducted at room temperature. At the beginning of a selection experiment, five individuals from the pooled larvae used in the experiment were introduced into each of three replicate dishes (5.3 cm diameter) of each of three sediment treatments and a seawater control. Dishes were filled to 1 cm depth with filtered seawater. The sediment treatments consisted of a ~1-cm-diameter patch of NBH Mud, Glass Beads or azoic mud from Sippewissett Marsh (Massachusetts) that was routinely used as food and substrate in the *Capitella* sp. I cultures. The dishes were examined after 5 min, and at regular intervals thereafter until the selection experiment concluded. The number of larvae still swimming in each dish was recorded, but these larvae were not removed. Shortly after the conclusion of a selection experiment, seawater control and Glass Beads dishes received small additions of mud from Sippewissett Marsh as substrate and food. After two days, sediments in all dishes were sieved over a 149 μm screen and surviving juvenile worms counted.

These tests permitted repeated comparisons of the number of experimental larvae that settled over time on sediments expected to be attractive (NBH Mud and Sippewissett Marsh mud), or unattractive (Glass Beads), as well as in the absence of a settlement cue (seawater control). Counts of settled juveniles in all treatments provided estimates of mortality at settlement for each larval batch. These mortality estimates were important because all samples from the sediment array were sorted live, which took two days to complete.

f. Hypotheses for selection experiments. Sediment selection experiments are arranged in Table 1 in groups according to the topic of study, and chronologically only within

these groups. The experiments fall into three general categories: 1) "All Mud" experiments, most of which tested for spatial larval settlement patterns in sediment arrays consisting of one sediment treatment, 2) "Checkerboard" experiments that tested for selection between two sediment treatments alternated in the sediment array in a checkerboard design, and 3) "Alternating Strip" experiments that qualitatively evaluated specific settlement behaviors in flow. Experiments in the first two categories were conducted both in still water and flow. Within all three categories, various experiments were conducted for specific purposes, either to evaluate an experimental condition or to test a specific hypothesis, as described below.

Five of the six All Mud experiments were conducted to test the null hypothesis of no difference in larval settlement among the rows or columns in the array. Deviations from random settlement may be due to: 1) addition method, 2) natural light gradients across the arrays (from the windows in the high bay), and 3) cross-stream flow effects in the flume (discussed in detail later). Thus, All Mud experiments were conducted in still water (Expts. 1 and 2) and in flow when the flume was in both orientations; that is, when the high-bay windows were parallel (Expts. 6 and 7) and perpendicular (Expt. 8) to the straightaway. Likewise, flow experiments were conducted when there were flow straighteners upstream only (Expt. 6) and both upstream and downstream (Expt. 7) of the array. These All Mud experiments were critical for interpreting spatial patterns in the Checkerboard experiments independent of treatment effects. All Mud Expt. 5 (methods described earlier) was conducted simply to determine if larvae actually circulated throughout the flume.

The Checkerboard experiments tested the null hypothesis of no difference in settlement between the two sediment treatments; the alternative hypothesis was selection for the NBH Mud treatment. Results of still-water Expt. 3, where there was highly significant selection for the NBH Mud over Glass Beads (Tables 2 and 6), permitted us to test the main question of this study: can larvae that are capable of selection in still water effectively execute this choice in flow? Six flow experiments were conducted using NBH Mud and Glass Beads. Experiments 9 and 10 were in cyclical flow. Experiment 10 lasted 12 h, compared to 2 h for all other selection experiments, to determine if experimental duration affected the results. The other four experiments (Expts. 11–14) were in steady flow, but Expt. 12 was conducted in the dark, and Expt. 14 used the four-by-four array. Still-water Expt. 4 and flow Expts. 15 and 16 were "cue-masking experiments," where a 4–5-mm-thick layer of Glass Beads (Expts. 4 and 16) or a 3-mm-thick layer of Barite (Expt. 15) was placed on top of the NBH Mud. The Barite layer simulated initial deposition of drilling muds adjacent to an oil production platform (e.g., Gettleson and Laird, 1980; NRC, 1983) prior to reworking by fauna or physical processes. The cue-masking experiments tested the hypothesis that larvae would still select the NBH Mud over the layered treatment if: 1) direct contact with a preferred sediment is required to elicit a settlement response and only surface characteristics are important in determining

sediment selection, or 2) a chemical substance initiating the settlement response in NBH Mud diffuses <3 mm (Expt. 15) or <4–5 mm (Expts. 4 and 16) up through the top layer of sediment in ~ 18 h.

The Alternating Strip experiments were conducted in flow only. Experiments 17–19 begin to address the second major question in this study: how might larval selection in flow be accomplished? These experiments were designed to qualitatively assess if larvae accepted or rejected sediment treatments while being transported downstream by the flow, as opposed, for example, to moving cross-stream among sediment treatments. This was prompted by laboratory observations of larval sediment-testing behavior in still water. Using the competency set-up, with one larva per dish, one sediment treatment per dish and bright room light, larvae were observed to swim up and down in the water, making direct contact with the sediment patch before swimming away. They usually settled after only one touch of a preferred sediment, although as many as four touches were sometimes required (Grassle *et al.,* 1992a). Thus we hypothesized that, in the field, larvae are transported to potential habitats by actively moving up and down while the flow carries them downstream. If they touch down on a favorable substratum, they generally settle immediately, but some of the larvae move back up into the water even after encountering a preferred sediment and make repeated tests as they are carried downstream. Multiple-testing larvae that encounter a favorable sediment usually settle after a maximum of four touches.

Experiments 17–19 were designed to test qualitatively this model for sediment selection in flow. We suggest that in our checkerboard array, larvae that repeatedly tested sediments while being carried downstream by the flow sometimes settled in Glass Beads because they were cued upstream by contacting NBH Mud. That is, one touch with an appropriate cue may initiate the process of settlement and metamorphosis even while larvae are still moving up and down between the sediment and the near-bottom water. In the field, the spatial extent of an "acceptable" habitat is likely to be of order 10's of meters to kilometers, depending on the sedimentary regime and distributions of other organisms. Thus, if larvae were cued to settle by contact with sediment at one location, but made a few more "hops" (being transported downstream only centimeters each time) before actually burrowing into the sediment, they would likely still be located within a patch of attractive sediment. This would not be the case in our laboratory sediment-selection experiments, however, because of the small spatial extent of our sediment patches. Settlement in the "wrong" sediment after having been cued by the "right" sediment may also have occurred in our still-water experiments, depending on the order in which the two sediment treatments were encountered.

To qualitatively test these ideas, we attempted to diminish the probability of larval settlement in the "wrong" sediment by alternating the NBH Mud and Glass Beads treatments in columns (i.e., five compartments per column in the five-by-five array) parallel to the flow direction (Expt. 17). In this case, larvae transported and testing

sediments only in the downstream direction would encounter the same treatment at each touchdown site along the array. In contrast, the two treatments were also alternated in rows (i.e., five compartments per row), both with NBH Mud at the leading edge (Expt. 18) and with Glass Beads at the leading edge (Expt. 19). In these two cases, we expected more settlement in Glass Beads compared to Expt. 17.

g. Statistical analyses for selection experiments. For the Checkerboard experiments, all larvae results, and sphere results only when there was >5% recovery in the array (see Table 2), were analyzed separately using the following ANOVA model, $y = \mu +$ Treatment + Row + Column + error, where μ is a constant. Interactions could not be tested because there were no replicates for each treatment, row and column location. The Row and Column effects were included to explain some of the variance due to location in the array, because these effects were sometimes significant in the All Mud experiments (Table 3). The residuals from the ANOVA model were tested for spatial autocorrelation using Moran's I and Geary's c statistics. If there was no significant positive spatial autocorrelation (see below), the ANOVA results are presented. When the Row or Column effect was significant ($p \leq 0.05$), Tukey's HSD multiple-comparisons tests were performed to determine which rows or columns differed. Data were log $(x + 1)$-transformed or $(\sqrt{x + 1})$-transformed, when necessary, to homogenize variances.

Spatial autocorrelation analysis (Cliff and Ord, 1981) was used in the Checkerboard experiments because the arrangement of treatments within the array was not random. Deviations from randomness violate the ANOVA assumptions of independence between treatments (rook's move hypothesis) and between replicates within a treatment (bishop's move hypothesis). The ANOVA assumes that residuals (in this case, the error remaining after Treatment, Row and Column effects have been removed) are independent and uncorrelated. When there is significant positive spatial autocorrelation of the residuals, the error term is underestimated and the Type I error will be greater than the nominal value for rejecting the null hypothesis ($p \leq 0.05$) (Cliff and Ord, 1981). Thus, the value for the computed test statistic is unreliable. For significant negative spatial autocorrelation, the error term is overestimated, the Type I error is less than the nominal value, and the statistical test is actually more conservative.

We used two different spatial autocorrelation statistics as a conservative measure because they utilize different information about the pattern of distribution (e.g., Sokal, 1979). Moran's I statistic is related to the product-moment correlation coefficient and is strongly affected by covariant departures from the mean. Neighbors with extreme values will make a large contribution to the magnitude of I, whereas neighboring values near the mean will make a small contribution. Moran's I ranges between -1 and 1 with the expected value close to 0; negative autocorrelation is

Table 3. Results of ANOVAs for "All mud" Expts. 1 and 2 in still water and Expts. 6-8 in flow (see text for ANOVA model). Results of Tukey's multiple comparisons tests are shown when Row or Column effect was significant at $p \leq 0.05$; horizontal bars connect means that are not significantly different. Means reported for Tukey's tests are untransformed data. Row 1 = leading edge of array; Column 1 = closest to outside flume wall.

Experiment 1

		Larvae			Spheres[α]		
Source	*df*	*SS*	*F*	*p*	*SS*	*F*	*p*
Row	3	835.25	3.00	0.088	3.246	8.15	0.006**
Column	3	302.25	1.09	0.403	0.584	1.465	0.288
Error	9	834.25			1.195		

Tukey's test

Row	1	2	3	4
$\bar{x}$	14.3	9.5	3.8	5.8

Experiment 2

		Larvae[α]			Spheres		
Source	*df*	*SS*	*F*	*p*	*SS*	*F*	*p*
Row	4	0.329	1.90	0.160	1020.00	7.81	0.001***
Column	4	0.476	2.74	0.065	881.60	6.75	0.002**
Error	16	0.694			522.40		

Tukey's tests

Row	2	1	3	4	5
$\bar{x}$	28.0	15.8	13.6	11.2	10.4

Column	4	3	1	2	5
$\bar{x}$	25.6	19.2	14.0	10.6	9.6

Experiment 6

		Larvae[α]			Spheres[α]		
Source	*df*	*SS*	*F*	*p*	*SS*	*F*	*p*
Row	4	6.578	21.47	0.000***	2.168	0.84	0.517
Column	4	1.528	4.99	0.008**	1.100	0.43	0.786
Error	16	1.225			10.271		

Tukey's tests

Row	1	2	3	4	5
$\bar{x}$	28.0	9.0	8.2	7.2	6.4

Column	5	4	3	2	1
$\bar{x}$	15.8	13.4	12.0	9.8	7.8

Table 3 (Continued)

Experiment 7

Larvae[a]

Source	*df*	*SS*	*F*	*p*
Row	4	6.394	11.46	0.000***
Column	4	2.416	4.33	0.014*
Error	16	2.231		

Tukey's tests

Row	1	2	3	4	5
$\bar{x}$	27.6	10.2	8.2	7.4	6.6

Column	5	4	3	1	2
$\bar{x}$	16.0	15.0	11.2	8.2	9.0

Experiment 8

Larvae[a]

Source	*df*	*SS*	*F*	*p*
Row	3	1.145	6.24	0.014*
Column	3	0.623	3.40	0.067
Error	9	0.550		

Tukey's tests

Row	1	2	3	4
$\bar{x}$	22.5	13.3	12.0	10.3

[a]log $(x + 1)$-transformed data.
*$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$.

when $-1 < I < 0$ and positive autocorrelation is when $0 < I < 1$. Geary's c statistic measures similarity of neighboring values as a distance function, regardless of the magnitude of deviations from the mean. That is, c is affected by absolute differences between cells and ranges from 0 to infinite with an expected value of 1. Negative autocorrelation is when $0 < c < 1$ and positive autocorrelation when $c > 1$.

For the All Mud experiments in the array, larvae and sphere results were analyzed separately using the following ANOVA model, $y = \mu + \text{Row} + \text{Column} + \text{error}$, where μ is a constant. Again, a Row X Column interaction could not be tested because there were no replicate compartments in each row and column location. A Tukey's HSD multiple-comparisons test was performed to determine which rows or columns differed when either of these main effects were significant ($p \leq 0.05$). Data were log $(x + 1)$-transformed to homogenize variances. Spatial autocorrelation (rook's and bishop's moves) of the residuals, with Row and Column effects removed,

was also done for the All Mud experiments to assess whether larvae naturally settle in these spatial patterns in the absence of a treatment effect.

Alternating Strip Expts. 17–19 and Expt. 5 were conducted for qualitative purposes only and were not amenable to statistics.

3. Results

a. Larval versus sphere recovery in the arrays. Independent of array design, 61.1–76.5% of the larvae added were recovered in the still-water arrays, and 6.8–26.6% in the flume arrays (Table 2). Sphere recovery in the arrays generally was higher in still water (11.1–61.3%) than in flow (0.3–4.4%, except Expt. 16, where sphere recovery was 23.3%) (Table 2). Sphere recovery was lower than larval recovery in all experiments except still-water Expt. 4, where sphere and larval recoveries were similar, and flow Expt. 16, where more spheres than larvae were recovered (Table 2).

In still water, because we attempted to add larvae and spheres only to the region of water directly above the array, an areal density of $\sim 3/cm^2$ would be expected if spheres fell and larvae fell or swam straight to the bottom. In fact, sphere and larval areal densities as a function of total sediment surface area in the arrays were 0.5–1.8 and 1.8–3.0/cm^2, respectively. These lower-than-expected sphere densities may be due to the particles actually being added to the water (or mixed by water disturbances) over a larger volume than targeted, or to rolling of spheres once they hit bottom. Assuming the latter was negligible, then sphere areal densities predict larval densities in the array due entirely to passive deposition. The generally higher larval than sphere areal densities suggest that the larvae actively located the array. Furthermore, larval areal densities in the NBH Mud treatment only were 2.3–3.6/cm^2. This suggests that larvae may have settled immediately if they happened to land on a preferred sediment when they first touched-down, but if an unpreferred sediment was first encountered, they actively left that site in search of a more favorable habitat.

In the flume, we added spheres and larvae upstream of the array at positions calculated to maximize the probability that they would hit the array on their first transit downstream. These calculations assumed that larvae and spheres fall in trajectories that can be predicted based on their still-water fall velocities and the mean flow speed at the addition height; that is, assuming that flow turbulence does not impede their descent. If, however, turbulent velocity fluctuations or other sources of vertical force on particles affect particle descent (e.g., Vanoni, 1946; Einstein and Chien, 1955; Coleman, 1981, 1986), then our calculations of addition positions were inaccurate or irrelevant (e.g., in the case where the particles actually remain suspended by the flow).

The 200 μm spheres used in the early experiments were selected to be within the range of the sinking rates of anesthetized *Capitella* sp. I larvae (Butman *et al.,* 1988a) and the steady, 5 cm s^{-1} flow was selected because it was the fastest flow that would not transport these spheres as bedload (i.e., rolling, hopping or saltating along the

bottom). This was determined by placing spheres directly on the flume bottom and observing their behavior as the flow was gradually increased to 5 cm s^{-1}. Under these conditions, the spheres did not move. We eventually determined (see below), however, that during the experiments, where spheres were added to the water column, most of them did not sink to the bottom but remained in suspended-load transport.

The repeated, poor recovery of the 200 μm spheres in the array (Table 2), even after adjusting the addition location several times, prompted us to determine where the spheres were actually contacting the flume bottom. Strips of grey "duct tape" were secured in place, with the sticky side of the tape facing up, across the flume channel to within ~1 cm of the flume walls and so that a width of ~4 cm was exposed to the overlying water. Eighteen strips were placed at ~1 m intervals around the flume, and were more closely spaced in the region of the test section and slightly farther apart around the bends. Nine of the locations were in the straightaway, four within the 1 m region encompassing the array. Twelve hundred spheres were added upstream of the array, as in the selection experiments, and after 30 min, the tape was covered with clear plastic-wrap and the flume drained. The number of spheres recovered on the strips was counted under a dissecting microscope. Only 14 spheres were recovered, distributed in ones and twos around the flume; only one sphere was recovered on the four strips closest to the array. This low recovery suggested that most of the 200 μm spheres did not sink to the bottom, but remained in suspended-load transport. This prompted use of larger spheres (270 and 383 μm) in subsequent experiments (Table 1).

The "sticky tape" experiment was repeated using the 383 μm particles. Three thousand particles were added and of the 44 recovered, 34 were located within the 1 m region encompassing the array. A total of seven spheres was found in the strips just up and downstream of the array region, and three spheres were found at the beginning of the downstream bend. Direct observations indicated that the larger spheres did not adhere as well as the 200 μm spheres to the tape, so recovery of the 383 μm spheres may be an underestimate. Furthermore, in this and many of the settlement experiments, some spheres were observed floating on the water surface. Nonetheless, these results suggested that at least some of the 383 μm spheres fell to the bottom within the region of the array in this flow. Direct observations of spheres on the bottom indicated that once landed, this flow did not transport them as bedload.

Recovery of the 383 μm spheres was not, however, appreciably better than recovery of the 200 μm spheres in the array, except in Expt. 16 (Table 2). Predictions of the number of spheres that should have been retrieved in the array are not possible because the way in which the spheres were added makes it impossible to know sphere concentration at any point in time or space. The implications of these results are discussed later (Section 4a.).

b. All Mud experiments. There was no significant spatial autocorrelation for the bishop's or rook's move for spheres or larvae in the All Mud, still-water experiments, indicating no natural tendency for larvae to settle in these spatial patterns. Sphere distributions in still-water, All Mud arrays showed a significant Row effect in Expt. 1 and significant Row and Column effects in Expt. 2 (Table 3). Both of these experiments were conducted with the still-water box on top of the flume after it had been turned perpendicular to the windows in the high bay (Table 1). In Expt. 1, row 1 (at the "leading edge," relative to the flume flow; orientation in still-water arrays is the same as in flume arrays) had significantly more spheres than rows 3 and 4, and in Expt. 2, row 2 had significantly more spheres than all other rows. Column 4 (column 5 is closest to the inside flume wall) had significantly more spheres than columns 1, 2 and 5 in Expt. 2. These results are likely due to addition technique and indicate the extreme difficulty in uniformly distributing particles in still water.

Based on sphere distributions in the All Mud, still-water experiments, significant Row and Column effects might be expected for larval settlement in still water due to methodologies alone. But, in fact, no significant Row or Column effects were detected for larval settlement in either Expts. 1 or 2 (Table 3; Fig. 3). Because larvae and spheres were added in the same way, the more uniform distribution of settled larvae than spheres suggests that some larvae did not simply fall or swim straight down to the bottom; alternatively, they may not have settled where they first landed.

In contrast to the still-water results, larval settlement distributions in the All Mud, flow experiments showed significant Row and Column effects in Expts. 6 and 7 (flume parallel to windows), and a significant Row effect in Expt. 8 (flume perpendicular to windows, four-by-four array) (Table 3; Fig. 3). Larval settlement was higher at the leading-edge row of the array and in the column closest to the inside flume wall. Even though the column effect was not significant in Expt. 8, about twice as many larvae were collected in the column nearest the inner than the outer flume walls (Table 4). As in still water, there was no significant spatial autocorrelation for the bishop's or rook's move. Higher larval settlement in sediment at the leading-edge row of the flume array is not surprising because this is the first sediment larvae encountered after they were released upstream, and in subsequent circuits. The reason for the cross-stream gradient is less intuitive, however, and may have been due to a cross-stream light gradient or to small-scale flow effects that redistributed suspended larvae in the cross-stream direction, as discussed below and later (Section 4b.). Sphere settlement was too low for meaningful statistical tests in these All Mud, flow experiments (Table 2), so we are unable to evaluate the extent to which the addition technique may have biased the larval settlement results.

Measurements of light energy incident on the plexiglass plate that contained the array (flume parallel to windows) indicated light gradients within the still-water box and the corresponding region of the flume containing the array. Throughout a cloudy day in March (Fig. 4), maximum light energy was measured in the "downstream"

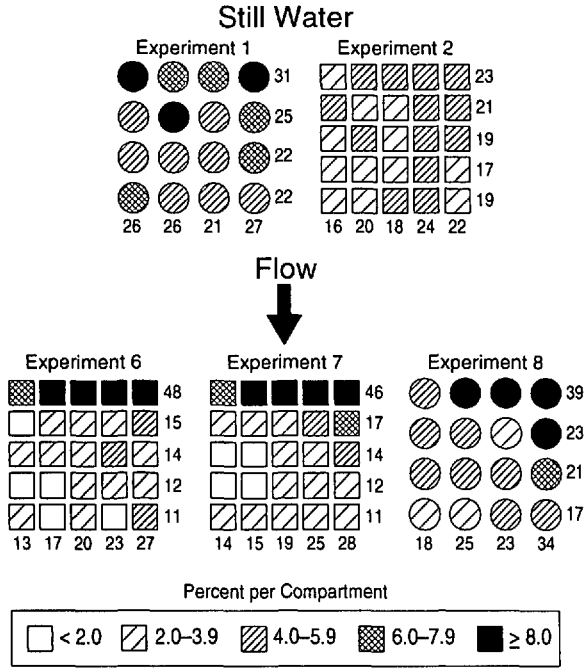


Figure 3. Spatial distribution of settled larvae in the All Mud experiments (see Tables 2 and 3). Plotted are the percentages of larvae collected in each compartment in the array; the percentages for the five compartments in each row and column are given to the right and bottom of the arrays, respectively. *N* (total number of larvae collected in the array) was 778 for Expt. 1, 918 for Expt. 2, 294 for Expt. 6, 300 for Expt. 7 and 232 for Expt. 8. Still-water and flume arrays are oriented in this figure as they were in the experiments, relative to the flume flow direction.

inside corner of the still-water box in mid-morning, when *Capitella* sp. I selection experiments were conducted, in the "upstream" inside corner in the early afternoon, and in the "downstream" inside corner near sunset. In the flume, maximum light energy was measured in the upstream inside corner throughout the day. On a sunny day in April, maximum light energy was measured in the upstream inside corner of both the still-water box and flume in mid-morning (data not shown). Thus, regions of highest light energy in the flume corresponded roughly with regions where the greatest number of larvae settled in the All Mud, flow experiments, suggesting a photopositive settlement response. Unfortunately, All Mud experiments were not conducted in still water before the flume was remodeled and rotated (Table 1).

An alternative explanation for the Column effect in flow is that, over time, a cross-stream gradient developed in the concentration of larvae in the water directly above the bottom, with more larvae near the inside flume wall. Thus, larval supply would have been greater on the inside than on the outside edge of the array. An

Table 4. Total number of larvae per column of the array and rank order (highest to lowest) by column (column 1 is closest to the outside flume wall). For checkerboard experiments, rank order is given only for columns 1, 3 and 5 because only these three columns had the same number of NBH Mud compartments (3 per column) and Glass Beads compartments (2 per column) (e.g., see Fig. 5). Significance of the column effect is also shown (see also Tables 3 and 6).

	Total by Column					Rank	Signifi-
	1	2	3	4	5	order	cance[a]
Still-Water Experiments							
All Mud							
1	42	57	54	79		4,2,3,1	
2	70	53	96	128	48	4,3,1,2,5	**
Checkerboard							
3	207	131	167	120	149	1,3,5	*
4	221	101	146	85	180	1,5,3	
Flow Experiments							
All Mud							
6	39	49	60	67	79	5,4,3,2,1	**
7	41	45	56	75	83	5,4,3,2,1	*
8	42	57	54	79		4,2,3,1	
Checkerboard							
9	14	10	19	16	22	5,3,1	
10	15	10	19	26	33	5,3,1	**
11	31	37	95	58	70	3,5,1	
12	23	25	38	44	91	5,3,1	
13	36	31	47	43	60	5,3,1	
14	25	51	115	133		4,3,2,1	
15	49	47	64	66	93	5,3,1	
16	18	16	25	17	48	5,3,1	

[a] $*p \leq 0.05$; $**p \leq 0.01$.

underlying mechanism that could produce this cross-stream gradient is the cross-stream circulation that occurs naturally around any bend (see Section 4b.).

Results of All Mud Expt. 5 (Table 5), conducted to determine whether larvae actually circulate throughout the flume, indicated that, indeed, some larvae traveled at least one complete circuit. Furthermore, even though larvae are added to the central 20 cm of the channel, they settled across the entire channel width. As in the other All Mud, flow experiments, there tended to be more larvae near the inner than the outer flume wall.

c. Checkerboard experiments. The Treatment effect was highly significant ($p \leq 0.001$) in all Checkerboard experiments (two in still water and eight in flow; Table 6), and in all cases, NBH Mud was the preferred treatment (Table 2). Neither the Row or Column effects were significant in still-water Expt. 4, but the Column effect was

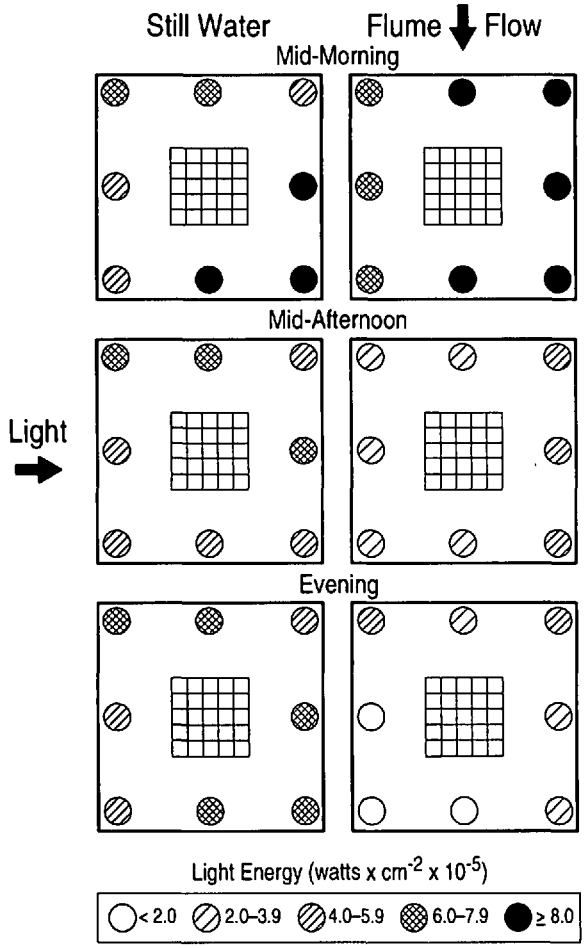


Figure 4. Light energy ([watts cm^{-2}] × 10^{-5}) measured at the corners and midway along the sides of the 50-cm-square plexiglass section containing the sediment array both in the still-water box and in the flume. Measurements were made at mid-morning (09:10–09:40), mid-afternoon (13:15–13:42) and early evening (16:53–17:26) on 30 March 1989 (a cloudy day). Flume flow direction and direction of light from windows in the high bay are shown in the legend. Still-water and flume arrays are oriented in this figure as they were in the experiments, relative to the flume flow direction.

significant in still-water Expt. 3, although there was no consistent pattern to the columns in which abundances were highest (Table 4). The Column effect was significant in flow Expt. 10, and the Row effect was significant in flow Expt. 16. Consistent with larval settlement in the All Mud, flow experiments, settlement was greater toward the inside flume wall and in the leading-edge rows of the array in Expts. 10 and 16, respectively (Table 6). Although the Column effect was statistically significant in only one of the seven Checkerboard, flow experiments using the

Table 5. Results of All Mud Expt. 5. The 48-cm-wide strips were divided into five regions for processing: "center" (20-cm-wide area corresponding to the array location), "flanks" (10 cm to either side of center) and "wall" (4 cm toward the wall from the flanks). Because these regions differ in surface area, both larval settlement per region and mean settlement per 16 cm^2 (in parentheses) are reported. Larvae were added 4 m upstream of the leading edge of the array.

	Cross-Stream Region ( ) = area in cm^2					
Row location	Outer wall (16)	Outer flank (40)	Center (80)	Inner flank (40)	Inner wall (16)	Total (192)
Leading edge of array	1 (1)	4 (1.6)	8 (1.6)	5 (2)	7 (7)	25
Downstream of array before bend	2 (2)	0 (0)	12 (2.4)	7 (2.8)	17 (17)	38
Upstream of paddle wheel after bend	2 (2)	5 (5)	7 (1.4)	1 (0.4)	3 (3)	18
Downstream of paddle wheel before bend	3 (3)	4 (1.6)	9 (1.8)	7 (2.8)	5 (5)	28
Upstream of array after bend	1 (1)	0 (0)	3 (0.6)	1 (0.4)	15 (15)	20
Total	9 (9)	13 (8.2)	39 (7.8)	21 (8.4)	47 (47)	129

five-by-five array, the rank order of columns 1, 3 and 5 (i.e., columns having the same number of NBH Mud and Glass Beads compartments) was the same (5, 3, 1) in six of these experiments, with highest abundances of larvae toward the inner flume wall (Table 4). Likewise, in Checkerboard, flow Expt. 14, using the four-by-four array, the rank order was 4, 3, 2, 1. In the one Checkerboard experiment where sphere settlement was >5% (Expt. 16), the Treatment effect was not significant, but there were significant Row and Column effects. Again, sphere abundances were higher in the leading-edge row and toward the inside flume wall (Table 6). There was no significant positive spatial autocorrelation for spheres or larvae in any of the Checkerboard experiments.

The consistent results among the seven checkerboard experiments (still water and flow) with NBH Mud and Glass Beads indicate that selectivity by *Capitella* sp. I larvae is relatively insensitive to the experimental conditions tested, including different flows (still, cyclical and steady), water temperatures (16.1–22.8°C), light regimes (mid-morning versus complete dark), experimental durations (2 and 12 h), times of the year, larval batches and experimental arrays (Table 1). Furthermore, mean settlement in NBH Mud was remarkably similar (17.3, 16.7, and 16.2) in the three steady-flow experiments that used the five-by-five array (Expts. 11, 12, and 13) and had identical flow regimes, but differed in various other experimental conditions (Fig. 5). Mean settlement in Glass Beads was very low (0.3–1.2) and similar between

still-water Expt. 3 and flow Expts. 9, 10, and 12–14, but flow Expt. 11 had approximately five times more larvae in the Glass Beads treatment than the other flow experiments, for no apparent reason.

The Treatment effect was highly significant in the cue-masking experiments, but mean settlement on Glass Beads covering NBH Mud in still water (Expt. 4) and on Barite covering NBH Mud in flow (Expt. 15) was high (7.6 and 10.0, respectively) relative to settlement in Glass Beads in most other Checkerboard experiments (Table 2).

d. Strip experiments. The *a priori* prediction that larvae would settle in higher numbers in Glass Beads (i.e., making the "wrong" choice) when exposed to alternating rows versus columns of NBH Mud and Glass Beads was qualitatively supported by results of Strip Expts. 17–19 (Tables 2 and 7). Only two larvae settled in Glass Beads compartments in Column Expt. 17, whereas 12 larvae settled in Glass Beads compartments in each of the Row experiments (Expts. 18 and 19). There was a cross-stream gradient in settlement in the Column experiment, with more larvae in the column near the inner flume wall, consistent with the All Mud, flow results (Table 3). Likewise, in Row Expt. 18, where the NBH Mud treatment was at the leading edge, settlement was over a factor of two higher in the first row than in each of the two downstream rows. In Row Expt. 19, where the Glass Beads treatment was at the leading edge, the first NBH Mud row contained only about 30% more larvae than the downstream row. Interestingly, in Row Expt. 18, nine larvae settled in the first Glass Beads row, which followed an NBH Mud row. In Row Expt. 19, however, not a single larva settled in the first Glass Beads row, at the leading edge of the array, but seven larvae settled in the next Glass Beads row downstream. This qualitatively suggests that upstream exposure to the NBH Mud treatment may have cued the larvae to settle, but some individuals made one or more additional "hops" before doing so and ended up actually settling in the Glass Beads rows downstream. This result can not be explained by passive transport of settled post-larvae because the boundary shear stress is not sufficient to resuspend bottom sediments (and, presumably, settled larvae within this sediment) and transport it downstream (pers. obs.).

e. Competency tests. Of the 15 larvae (five per dish) observed in each treatment of the competency tests, none of them spontaneously settled in the seawater control even after 90 min. In the Glass Beads dishes, a range of one to five, but usually only one larva settled during this time. In contrast, 14 of the larvae had usually settled within 5 min of addition to the NBH Mud and Sippewissett Marsh mud dishes, and all 15 were usually settled 25 min later. Juvenile survival for 2 d beyond the selection experiments was usually 93–100%, and never dropped below 73%, with no consistent differences among the treatment dishes.

Table 6. Results of ANOVAs for "Checkerboard" Expts. 3 and 4 in still water and Expts. 9-16 in flow (see text for ANOVA model). See caption to Table 3 for further explanation.

Experiment 3

		Larvae[α]		
Source	*df*	*SS*	*F*	*p*
Treat	1	242.60	1006.61	0.000***
Row	4	1.48	1.53	0.244
Column	4	3.54	3.67	0.028*
Error	15	3.62		

Tukey's test

Column	1	3	5	2	4
$\bar{x}$	41.4	33.4	29.8	26.2	24.0

Experiment 4

		Larvae[β]			Spheres		
Source	*df*	*SS*	*F*	*p*	*SS*	*F*	*p*
Treat	1	16.89	137.25	0.000***	500.27	4.20	0.058
Row	4	1.23	2.49	0.087	1411.30	2.96	0.055
Column	4	1.12	2.26	0.110	825.76	1.73	0.195
Error	15	1.85			1788.37		

Experiment 9

		Larvae[β]		
Source	*df*	*SS*	*F*	*p*
Treat	1	11.71	43.50	0.000***
Row	4	0.58	0.54	0.710
Column	4	0.22	0.20	0.932
Error	15	4.04		

Experiment 10

		Larvae[β]		
Source	*df*	*SS*	*F*	*p*
Treat	1	20.94	265.28	0.000***
Row	4	0.54	1.72	0.198
Column	4	1.98	6.26	0.004**
Error	15	1.18		

Tukey's test

Column	5	4	3	1	2
$\bar{x}$	6.6	5.2	3.8	3.0	2.0

Table 6 (Continued)

Experiment 11

Larvae$^{\beta}$

Source	*df*	*SS*	*F*	*p*
Treat	1	7.209	19.12	0.000***
Row	4	1.948	1.29	0.317
Column	4	3.997	2.65	0.074
Error	15	5.656		

Experiment 12

Larvae$^{\beta}$

Source	*df*	*SS*	*F*	*p*
Treat	1	33.91	122.72	0.000***
Row	4	2.91	2.64	0.076
Column	4	1.72	1.56	0.236
Error	15	4.14		

Experiment 13

Larvae$^{\beta}$

Source	*df*	*SS*	*F*	*p*
Treat	1	35.84	196.04	0.000***
Row	4	1.82	2.49	0.087
Column	4	0.32	0.44	0.779
Error	15	2.74		

Experiment 14

Larvae$^{\beta}$

Source	*df*	*SS*	*F*	*p*
Treat	1	35.70	114.09	0.001***
Row	3	0.70	0.74	0.556
Column	3	2.19	2.33	0.151
Error	8	2.50		

Experiment 15

Larvae$^{\beta}$

Source	*df*	*SS*	*F*	*p*
Treat	1	0.517	0.52	0.038***
Row	4	0.691	1.74	0.194
Column	4	0.882	2.22	0.116
Error	15	1.491		

Table 6 (Continued)

Experiment 16

		Larvae[β]			Spheres[β]		
Source	*df*	*SS*	*F*	*p*	*SS*	*F*	*p*
Treat	1	22.64	198.07	0.000***	0.06	0.16	0.692
Row	4	1.92	4.19	0.018*	8.00	5.55	0.006**
Column	4	0.66	1.44	0.268	13.68	9.48	0.000***
Error	15	1.71			5.41		

Tukey's test

Row	1	3	5	2	4
$\bar{x}$	9.8	4.8	4.2	4.4	1.6

Tukey's test

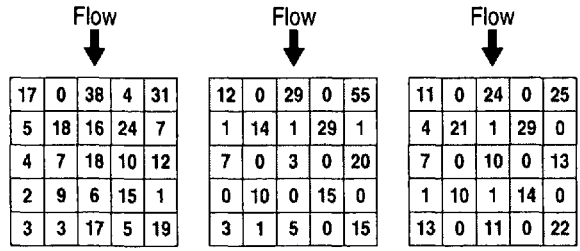
Row	1	2	3	4	5
$\bar{x}$	23.6	18.2	6.0	4.8	3.4

Column	4	5	3	2	1
$\bar{x}$	26.0	11.8	11.6	5.0	1.6

[α]$\sqrt{x+1}$-transformed data.
[β]$\log(x+1)$ - transformed data.
*$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$.

4. Discussion

Capitella sp. I larvae were highly selective for a natural, organic-rich, muddy sediment as opposed to an abiotic, low-organic alternative in all two-choice, still-water and flow experiments. This preference is consistent with adult field distributions (see Introduction). It is also consistent with results of laboratory studies showing that the quality and quantity of organic matter affects juvenile and adult growth rates (Tenore, 1977a, b; Tenore and Hanson, 1980; Tenore and Chesney, 1985; Grémare *et al.,* 1988; Marsh *et al.,* 1989; Tsutsumi, 1990) and reproductive output (Chesney and Tenore, 1985; Grémare *et al.,* 1988, 1989a,b). Active selection for a favorable feeding environment for adults by the non-feeding larval stage suggests that larval characteristics that facilitate location of organic-rich habitat may have adaptive value to this species. Studies of laboratory populations of *Capitella* sp. I have also shown that population cycles are driven by food supply and larval recruitment and mortality (Chesney and Tenore, 1985; Grémare *et al.,* 1989a,b), and that populations are sensitive to fluctuations in food availability, with the ability to rapidly adjust their reproductive rates accordingly (Grémare *et al.,* 1988). Active and immediate response to favorable habitat by larvae settling from the plankton would also enable an opportunistic species to quickly colonize a newly disturbed locale. Likewise, active and immediate response of opportunistic larvae, like those of



Date of Experiment	4 / 22 / 87	6 / 24 / 87	7 / 15 / 87
Water Temperature	17.5 °C	20.5 °C	22.8 °C
Water Salinity	31.5 ‰	32.2 ‰	32.3 ‰
Time of Experiment	13:45 – 15:45	01:30 – 03:30	10:30 – 12:30
No. Larvae Added	1200	1200	1200
No. Larvae in Array	291	221	217
No. in NBH Mud (N=13) $\bar{x} \pm 1$ *S.D.*	17.3 ± 9.8	16.7 ± 14.3	16.2 ± 7.1
No. in Beads (N=12) $\bar{x} \pm 1$ *S.D.*	5.5 ± 4.3	0.3 ± 0.5	0.6 ± 1.2

Figure 5. Number of larvae per compartment of the array for Checkerboard, flow Expts. 11 (left), 12 (middle) and 13 (right). Dark squares are the NBH Mud treatment and light squares are the Glass Beads treatment.

Capitella sp. I, that are competent and will settle (when cued) upon release from the female brood tube, would facilitate rapid local build-up of the population for exploitation of labile resources (e.g., Chesney and Tenore, 1985; Grémare *et al.*, 1989a).

Larval sediment selectivity was insensitive to a variety of experimental conditions, including variations in water temperature, light regime, experimental duration, distance sediment treatments were separated, time of year and larval batch. Selective settlement also occurred relatively quickly (within 2 h). Selectivity was similar in experiments conducted in steady and cyclical flows, and only about 2% more larvae settled in the 12 h (Expt. 10) versus 2 h (Expt. 9) cyclical flow experiments. Furthermore, results of competency tests indicated that for most larvae, settlement and metamorphosis occurred within 5 min of encountering a preferred sediment. The following characteristics of *Capitella* sp. I larvae are likely responsible, at least in part, for the consistent selectivity results among experiments: the lecithotrophic larvae 1) are competent upon release from the female brood tube, 2) show a very quick and consistent settlement response when cued, 3) remain selective for up to five days with no detectable decrease in early juvenile survival (Grassle *et al.*, 1992a) and 4) actively swim down and remain near the bottom (at least in still water, but see later discussion).

Results of the cue-masking experiments (Expts. 4, 15 and 16) indicate that either direct physical contact with the sediment was required to elicit a settlement response, or if larvae responded to a soluble chemical, the cue did not diffuse 3–5 mm

Table 7. Results of Strip experiments where NBH Mud and Glass Beads were alternated in columns (Expt. 17) or rows (Expts. 18 and 19). Total number and $\bar{x} \pm 1$ SD of larvae per column or row are presented; in each case $N = 5$ compartments. Column 1 is closest to the outside flume wall and row 1 is upstream, relative to the flow direction.

	Columns (Expt. 17)				
	1 (mud)	2 (beads)	3 (mud)	4 (beads)	5 (mud)
Total	20	0	29	2	37
$\bar{x} \pm 1$ SD	4.0 ± 2.7	0	5.8 ± 3.6	0.4 ± 0.5	7.4 ± 1.1
	Rows (Expt. 18)				
	1 (mud)	2 (beads)	3 (mud)	4 (beads)	5 (mud)
Total	54	9	26	3	21
$\bar{x} \pm 1$ SD	10.8 ± 5.3	1.8 ± 1.6	5.2 ± 2.5	0.6 ± 0.9	4.2 ± 2.3
	Rows (Expt. 19)				
	1 (beads)	2 (mud)	3 (beads)	4 (mud)	5 (beads)
Total	0	39	7	30	5
$\bar{x} \pm 1$ SD	0	7.8 ± 5.1	1.4 ± 1.1	6.0 ± 5.3	1.0 ± 1.2

up through the sediment within 18 h. The first explanation is most likely given the paucity of evidence for invertebrate larvae settling in response to soluble compounds, independent of direct contact (e.g., Pawlik, 1992), and our observations of *Capitella* sp. I settlement behavior. Substantially higher settlement in NBH Mud compartments in the leading-edge rows of all flume arrays also indicates that many larvae may make the decision to settle upon first encounter with a favorable substratum.

The low settlement of larvae in NBH Mud covered by a 3-mm-thick layer of barite (Expt. 15) suggests that larvae may avoid settling in an area where large amounts of barite have been deposited. Laboratory experiments have also shown that adult *Mediomastus ambiseta,* another opportunistic, capitellid polychaete, actively migrated out of 100% barite in favor of NBH Mud (Starczak *et al.,* 1992). Barite (94–96% $BaSO_4$) is the most abundant, inert, mineral component of drilling muds. Drilling muds are used, among other things, to lubricate the drill bit during offshore oil exploration and production, and are discharged as waste at the sea surface. Mass particulate concentrations of barium (barite = 59% barium) can be 10 to 20 times above ambient concentrations near a drill site (e.g., barium concentrations in excess of 40,000 ppm were recorded in the Gulf of Mexico production drilling area; Petrazzuolo, 1983), but decrease rapidly with distance from the point of discharge (e.g., Neff, 1987; Neff *et al.,* 1989). Thus, our experiments are probably relevant only

to regions very close to production drilling platforms, and immediately after discharge and deposition, before biological and physical processes can bury, mix or transport the deposited material. Long-term (10 wks), laboratory studies in flow-through aquaria of the effects of barite on meiofauna (Cantelmo *et al.*, 1979) and macrofauna (Tagatz and Tobia, 1978) colonization also indicated significantly less colonization of sand covered by a 5-mm-thick layer of barite.

a. Spheres as passive larval mimics. Plastic spheres with sinking rates within the range of gravitational fall velocities and downward swim speeds of *Capitella* sp. I larvae were used in these experiments as a first step toward evaluating when and how larval behaviors are involved in the sediment-selection process. We achieved similarity only in the vertical velocity of the particles and larvae in these initial experiments because scaling arguments have indicated that matching w/u_*, where w is the still-water gravitational fall velocity, is one criterion for satisfying dynamical similarity of particle behavior in boundary-layer flow (e.g., Butman *et al.*, 1986; Nowell and Jumars, 1987). The larval mimics we selected, smooth polystyrene spheres, may not, however, adequately mimic larvae sinking or swimming toward the bottom because of differences between the larvae and spheres in density, size and surface characteristics (e.g., shape, roughness, surface charge). Results of this study were expected to help determine if more sophisticated larval mimics, dictated by scaling parameters other than just w/u_*, would be required in subsequent studies. We had not anticipated, however, that locations where spheres (and larvae) were added to the water could be a confounding factor in interpreting the flume results. In fact, the behavior of relatively large, low-density particles in flow is more complicated than we realized and findings (by other workers, as described below) published subsequent to our experiments shed new light on potential reasons for the poor recovery of our mimics in these flume experiments, as well as providing additional guidance for the selection of more meaningful passive mimics in the future.

The intent here was to use sphere abundances and distributions in the array as the null model for initial larval settlement distributions due to passive sinking, as in Eckman (1983, 1990), Hannan (1984), Wethey (1986), Ertman and Jumars (1988), Mullineaux (1988), Butman (1989), Eckman *et al.* (1989) and Garland and Mullineaux (1992) or direct, downward swimming, as Pawlik *et al.* (1991). Such a comparison between sphere and larval abundances and distributions in the array was meaningful and revealing in our still-water experiments. The generally higher larval than sphere abundances in the arrays and in the NBH Mud versus Glass Beads treatments suggests that larvae actively located the array, settled in the NBH Mud treatment when it was encountered, and actively left the Glass Beads treatment if they happened to first land on it or during subsequent searches.

In the flume, however, the spheres clearly did not simply sink through the water column in trajectories that could be accurately predicted based on still-water

gravitational fall velocities of the spheres and flow speed at the height of sphere introduction. In fact, it appears that most of the 200 μm spheres remained in suspended-load transport and that paths of even the largest spheres (mean diameter of 383 μm) were evidently affected by flow turbulence. In retrospect, this is not surprising given observed paths of even relatively dense, cohesionless sediment grains in turbulent, flume flows (e.g., Vanoni, 1946; Einstein and Chien, 1955; Sumer and Oğuz, 1978; Coleman, 1981, 1986; Sumer and Diegaard, 1981) and the recent experimental and theoretical studies of the hydrodynamic-retarding forces and effects on finer or lower-density particles in turbulent flows (e.g., Self *et al.,* 1989; Dade *et al.,* 1991; Dade, 1992; Hill, 1992).

Particularly relevant is Dade's (1992) study of settling retardation of hydrodynamically large particles ($R_p < 1$; where R_p is a particle Reynolds number, du_*/ν, d is the nominal spherical diameter of the particle and ν is the kinematic fluid viscosity) that respond to turbulent fluctuations in the flow (i.e., w/u_* "much less than unity"). Particles within this parameter space sink at slower rates, relative to still-water fall velocities, due to turbulent fluctuations in the flow that produce dynamical asymmetry of the drag on the particle. Dade (1992) showed that the magnitude of sinking retardation (over vertical distances to within 1 cm of the bottom) due to turbulence of particles with relative densities ($\rho_r = \rho_p/\rho_f$, where ρ_p is particle density and ρ_f is fluid density) of $1.01 \leq \rho_r \leq 2.65$ is a function of both w/u_* and R_p. Thus, for 383 μm, polystyrene spheres ($\rho_p = 1.05$ g cm^{-3}) in a flow with u_* of 0.26 cm s^{-1}, the ensemble-averaged "effective" fall velocity would be ~80% of the still-water fall velocity. This provides at least a partial explanation for why so few spheres were collected in the array; that is, because our addition locations were calculated based on still-water fall velocities that may have been overestimated by ~20%. Dade (1992) also showed that below a height of 1 cm above the bed, interactions between short-lived turbulent eddies and particles result in additional acceleration effects that can further reduce sinking; these effects are largest for relatively low-density particles ($\rho_r < 1.03$) with diameters <100 μm and $u_* \geq 1$ cm s^{-1}, and may be negligible for the spheres, but not necessarily the larvae (i.e., Dade's study was on spherical, smooth particles only), used in this study.

These results suggest that, at the least, matching both particle size and fall velocity is required to satisfy dynamical similarity between passively sinking or downward swimming larvae and particles. Furthermore, hydrodynamic reduction of sinking rates of very low-density particles with complex surfaces, like invertebrate larvae, has not been explored. It is not known, for example, what size dimension of larvae is relevant for calculating R_p of larvae. Thus far, in all studies (cited earlier) that have used passive larval mimics, particles were selected to match only fall velocity or downward swim speed of the larvae.

In our flume studies then, at best, only qualitative observations can be derived from sphere versus larval distributions. That is, if we assume that *Capitella* sp. I

larvae and spheres experienced similar drag reduction for sinking to within 1 cm of the bed, and that there was no additional reduction in sinking over the last 1 cm, then our only error is in calculating the positions for adding larvae and spheres to the water to maximize the probability that they would encounter the array during their first circuit. In fact, because of the 20% reduction in "effective" fall velocity indicated by Dade (1992), neither the spheres nor the larvae should have settled in the array on the first pass. Thus, because substantial numbers of larvae were collected in the array, but the 200 μm spheres (mean fall velocity within the range of passively sinking *Capitella* sp. I larvae) remained in suspended-load transport, larvae clearly must have actively swum down to reach and remain near the bottom in this flow. Likewise, because the 383 μm particles theoretically (i.e., according to Dade, 1992) sank slower than expected (based on still-water gravitational fall velocities) and thus were transported past the array before hitting bottom, larvae either swam down in flow at velocities faster than those of the spheres, or larvae entered the array largely during circuits subsequent to their first pass over the array (during 2 h, water circulates about 15 times around the flume racetrack). Furthermore, in Expt. 16, where for unknown reasons about 10 times more 383 μm spheres were recovered in the array than in any other experiment, the Column effect was significant (Table 6) and cross-stream sphere distributions were similar to cross-stream distributions of larvae (Tables 3 and 4). This suggests that although larvae probably reached and stayed near the bottom by active swimming, they were initially distributed within the array like passive particles (e.g., as in Pawlik *et al.,* 1991). In general, however, detailed, direct observations of individual particles and larvae in flow are required to determine the extent to which initial delivery to the bottom is controlled by larval behaviors or physical processes.

b. Larval settlement and selectivity in flow. Results of the flume experiments clearly indicate that *Capitella* sp. I larvae are capable of active sediment selection in flow, thus answering the first question posed in this study (see Introduction). The second question, concerning how selection in flow might be accomplished, was only cursorily addressed here, but all results are consistent with a single model (discussed below). Although the flow used here was near the mid-point of the range for turbulent, tidal flows in shallow coastal embayments where this species can be abundant, it is a very weak flow relative to the full spectrum of flows (e.g., tidal-, density- and wind-driven circulations) that may occur in these environments (e.g., B. Butman *et al.,* 1988; Geyer and Signell, 1990). Yet even in this weak flow, mean horizontal flow speeds well-exceeded horizontal swim speeds of *Capitella* sp. I larvae (measured in still water; Butman *et al.,* 1988a) within larval search distances of the bottom (Butman, 1986). This suggests that larvae were unlikely to have actively selected a preferred sediment by a mechanism that required swimming horizontally upstream against the flow.

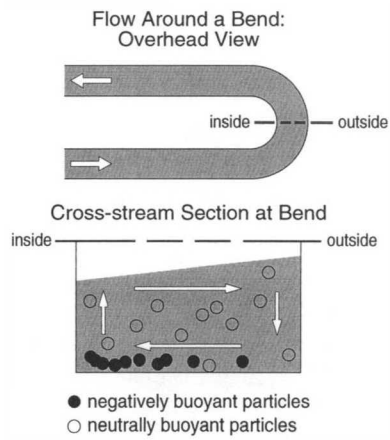


Figure 6. Diagram illustrating particle behavior in cross-stream flow around at bend (see text).

The model we suggest for active habitat perusal in the field by *Capitella* sp. I larvae, based on our direct observations in still water and qualitative experiments, is a near-bottom "skimming" trajectory—larvae swimming vertically up and down while they are being transported by the flow, and testing sediment on contact. Results of the Strip experiments (Table 7) qualitatively support this model. There is also qualitative support for the hypothesis that larvae not settling in a preferred substratum after initial contact may, nonetheless, be "conditioned" by their first encounter with this sediment and eventually settle downstream, irrespective of the sediment at the final touchdown site. Thus, whereas nine larvae settled in the first Glass Beads row, which followed an NBH Mud row in Strip Expt. 18, not a single larva settled in the first Glass Beads row, at the leading edge of the array in Strip Expt. 19. Seven larvae settled, however, in the next Glass Beads row downstream, having potentially encountered the NBH Mud row in-between.

The Column effect was significant for larvae in two of the three All Mud, flow experiments (Table 3) and one of the Checkerboard, flow experiments (Table 6) with more larvae settling toward the inside flume wall. Similar, cross-stream gradients were indicated (although they were not statistically significant) in all other flume experiments except Expt. 11, but not in any of the still-water experiments (Table 4). The observed cross-stream gradient in larval settlement may be explained by cross-stream redistribution of suspended larvae (initially approximately uniformly distributed), resulting in a cross-stream gradient in larval supply to the array. The mechanism for redistribution would be the cross-stream circulation that occurs in the bends of any curved, steady-flow channel due to a cross-stream pressure gradient (e.g., Henderson, 1966, p. 252). Water depth is greater on the outside than the inside of the bend (refer to Fig. 6) and because the along-channel flow is very slow at the bottom (due to the drag of the bottom on the flow), this pressure gradient drives a

cross-stream flow toward the inner flume wall along the bottom. To balance mass, there is a return flow toward the outer flume wall at the water surface. Because the mean along-channel flow carries the water downstream, a characteristic corkscrew-like, cross-stream circulation develops around the bend; the magnitude of the cross-stream velocities decrease as the flow moves down the straightaway. The flow straighteners were installed to limit this circulation to smaller cells, but it cannot be eliminated completely as long as there is a bend. Cross-stream flow toward the inner flume wall in water just above the bottom of the Paddle-Wheel Flume was confirmed using dye (pers. obs.).

The behavior of particles in this cross-stream flow depends on their fall velocities relative to the velocity of the upward flow along the inner flume wall (Fig. 6). If particles are so negatively buoyant that they cannot be carried up at the inner flume wall, they will tend to concentrate toward this wall over time. If particles are sufficiently buoyant to be entrained by the upward flow, they will move cross-stream toward the inner wall along the bottom, then up, then cross-stream toward the outer wall at the surface, and then back down again. This circulation results in no net redistribution of particles.

The cross-stream distribution of settled *Capitella* sp. I larvae in the flume arrays is consistent with hydrodynamic redistribution of negatively buoyant particles. The cross-stream gradient in larval settlement in the array, for experiments where the flume was parallel to the high-bay windows (see Table 1), could also be explained by a cross-stream light gradient (Fig. 4). However, because light gradients were similar in still-water and flow, a "cross-stream" gradient, with more larvae toward the inner flume wall, would also be expected in still water, and this did not occur (Tables 3 and 4). Furthermore, other studies of *Capitella* sp. I settlement in the Paddle-Wheel Flume, after it had been rotated perpendicular to the windows, also showed a significant Column effect similar to that observed here (Grassle *et al.*, 1992a; Snelgrove *et al.*, 1993).

If the cross-stream distribution of larvae in the flume arrays was due to a cross-stream flow effect, this implies that larvae were not distributed throughout the water column but remained very close to the bed by active swimming (i.e., they acted like the negatively buoyant particles depicted in Fig. 6). Confinement of larvae to the viscous sublayer due to shear-induced torque, as recently suggested by Jonsson *et al.* (1991) for cockle (*Cerastoderma edule*) larvae, is unlikely to be applicable to *Capitella* sp. I larvae because the mechanism requires an asymmetrical density distribution (i.e., provided by the umbo of the bivalve shell) and upward-directed, spiral swimming behavior. *Capitella* sp. I larvae possess neither of these characteristics. Redistribution of larvae by cross-stream circulation in the flume can be viewed as a generic effect of relatively weak flows on movement of *Capitella* sp. I larvae located in the water just above the bottom, and suggests that suspended larvae of this species may be passively transported even by relatively weak flows.

The cross-stream distribution of 383 μm spheres in Expt. 16, where the Column effect was significant, indicated higher sphere abundances in columns 4 and 5, closest to the inside flume wall (Table 6). These results indicate that cross-stream redistribution may occur even due to flows in the straight channel approaching the array (i.e., because the 383 μm spheres are not expected to recirculate). In fact, very weak cross-stream flow in the straightaway containing the array were indicated by direct observations (dye studies) and by vertical velocity profiles (Appendix). Thus, although results of Expt. 5 indicated that some larvae traveled at least one circuit around the flume (Table 5), recirculation is not required to explain larval settlement patterns in the array. This underscores the necessity for very careful documentation of flume flow characteristics for interpreting results of larval transport and settlement experiments in flumes.

Cross-stream flow in the flume need not affect all larval species similarly, particularly because larval entrainment in such a flow is a function of the "effective" fall velocity (whether due to active swimming or passive sinking) of the larva (e.g., Fig. 6). In the Paddle-Wheel Flume, a similar Column effect, with more larvae toward the inner flume wall, was detected for larvae of the polychaete *Phragmatopoma lapidosa californica* (Pawlik *et al.,* 1991), but not for larvae of the bivalves *Mulinia lateralis* (Grassle *et al.,* 1992b; Snelgrove *et al.,* 1992) and *Mercenaria mercenaria* (Butman *et al.,* 1988b). Competent larvae of *P. lapidosa californica,* like those of *Capitella* sp. I, were observed to swim to the bottom of the water column, and appeared to have remained there, in certain flows (Pawlik and Butman, submitted), but active swimming by competent *M. mercenaria* larvae tended to make them neutrally buoyant in flow (C. M. Webb and Butman, unpublished). Late pediveligers of *M. lateralis,* however, have been observed to stay close to the bottom in still water (Grassle *et al.,* 1992b), so the absence of a cross-stream flow effect for this species cannot presently be explained.

c. Ecological implications. Quantitative experiments in this laboratory flume study of *Capitella* sp. I settlement and sediment selectivity indicate that larvae were selective in flow when given a choice between highly contrasting sediment treatments. There is also qualitative support (from several kinds of experiments) for the hypothesis that competent larvae of this species do not passively sink to the bottom, but actively swim down and remain in near-bottom waters until settlement, at least in the relatively slow, turbulent flow tested here. They may be initially delivered to the bed like passive particles (see also Snelgrove *et al.,* 1993) or they may periodically swim out of suspension; once on the bottom they are presumed to test sediment on contact. We propose that sediment choices may be constrained by hydrodynamical processes; larvae "choose" a substratum by electing to stay or leave sediments to which they are exposed as they are transported downstream. Thus, even relatively weak flows, such as cross-stream circulation in a racetrack design flume (cross-stream flow that is

weaker than the depth-integrated, mean flow speed in the flume), may affect larval distributions in near-bottom waters and thus, larval supply to the bed. The susceptibility of *Capitella* sp. I larvae in near-bottom waters to passive transport suggests that there may be an upper limit to the flows in which these larvae can settle, as demonstrated for *Phragmatopoma lapidosa californica* larvae (Pawlik and Butman, submitted), but this limit has yet to be determined for *Capitella* sp. I (Grassle *et al.,* 1992a).

These results suggest that active sediment selection by settling *Capitella* sp. I larvae may be responsible, at least in part, for field distributions of this species. Results of earlier experimental field studies indicating passive larval transport (Hannan, 1984; Butman, 1989) and delivery to the bed (Eckman, 1979, 1983) or hard substrates (Wethey, 1986; Mullineaux and Butman, 1990, 1991; Pawlik *et al.,* 1991; Pawlik and Butman, submitted), and the results of this study and our other studies of larval settlement of infaunal species in flume flows (Butman *et al.,* 1988b; Grassle and Butman, 1989; Grassle *et al.,* 1992a,b; Snelgrove *et al.,* 1993), suggest that larval supply to the bed may be determined largely by hydrodynamical processes; once deposited, however, larvae may actively affect their local distributions by opting to stay or leave. These decisions may be based on responses to either positive or negative cues (see Woodin, 1991); this study was not designed to distinguish between these alternatives.

The two sediment choices presented to the larvae in this study were unrealistic for the field, because two sediments with such different percentages of organic matter are unlikely to occur naturally over such small spatial scales. However, subsequent flume experiments with *Capitella* sp. I larvae and sediments that differed more subtly (but were still offered over small spatial scales) also indicated sediment selectivity in flow (Grassle *et al.,* 1992a). Larger-scale flume and field experiments are required to elucidate the full range of conditions over which larvae can effect habitat choice.

Active sediment selection by larvae in still water and flume flows has likewise been demonstrated for two other opportunistic infaunal organisms with relatively distinct distributions relative to sediment type, *Capitella* sp. II (Grassle and Butman, 1989) and *Mulinia lateralis* (Grassle *et al.,* 1992b; Snelgrove *et al.,* 1993). Larval sediment selectivity was not demonstrated in still water (Bachelet *et al.,* 1992) or flow (Butman *et al.,* 1988b), however, for *Mercenaria mercenaria,* a species with relatively low habitat affinity in adult distributions. It is thus possible that sediment selectivity by settling larvae of opportunistic species may be an adaptive trait for quickly exploiting newly disturbed habitat. Larval sediment selectivity is not likely to be limited to opportunistic infaunal organisms, particularly given the mounting evidence for habitat selectivity in flow by hard-substrate species with a range of life history characteristics (e.g., review of Crisp, 1984; also Mullineaux and Butman, 1991; Pawlik *et al.,* 1991; Walters, 1992; and others). The adaptive significance of substrate selectivity may differ among species and depend on the time-scale of response

relative to the competency period, the effectiveness of habitat location as a function of flow regime, and the overall degree of substrate specificity, all of which are likely to vary as a function of life-history characteristics and species distributions. Moreover, sediment selectivity by settling larvae of infaunal organisms does not preclude post-settlement phenomena from further restricting adult distributions (e.g., Muus, 1973; Wilson, 1980; Luckenbach, 1984; Woodin, 1985; Peterson, 1986; Watzin, 1986).

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APPENDIX

Vertical profiles of velocity were taken at three along-channel positions (middle of the array, and 1 and 2 m upstream of this point) in the center of the channel, and at four additional cross-stream positions (7.5 and 15 cm to either side of the flume centerline) at the array. Horizontal velocity was measured with a single-axis, forward-scatter, laser-Doppler velocimeter (LDV; Thermal Systems Instruments) in runs without larvae but with the same water depth and paddle-wheel rotation used in the selection experiments. Flow behavior was evaluated relative to theoretical expecta-

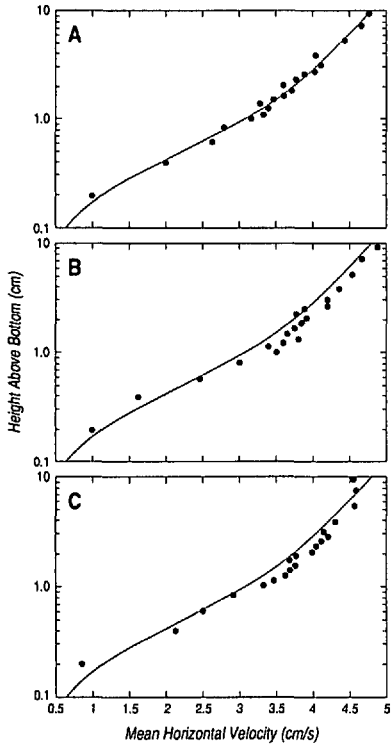

Figure A.1. Profiles of mean horizontal velocity (dots) taken along the flume centerline in the middle of the array (A), 1 m upstream (B) and 2 m upstream (C) of the array. The solid curve is the fit of the velocity profile in A to a semi-empirical expression for mean velocity in a steady, open-channel flow above a hydrodynamically smooth bottom (see text).

tions using a semi-empirical expression for the mean velocity in a steady, open-channel flow above a smooth bottom

$$u = u_* f\left[\frac{zu_*}{\nu}\right] + u_* \frac{2\Pi}{\kappa} \sin^2\left(\frac{\pi z}{2h}\right)$$

(Nezu and Rodi, 1986), where u is mean horizontal velocity, u_* is boundary shear velocity, z is height above bottom, ν is kinematic viscosity, Π is the empirical Coles parameter which determines the strength of the wake correction, κ is von Karman's constant (0.4) and h is water depth. The first term on the right-hand side is the universal velocity distribution near a smooth wall based on the empirical expression proposed by H. Reichardt (see Landahl, 1967), and the second term is the wake correction introduced by Coles (1956). This technique for obtaining u_* results in an error in the estimate of about 5% (J. H. Trowbridge, pers. comm.). Mean velocity measurements were fit to this equation by a least-squares regression, using u_* and Π

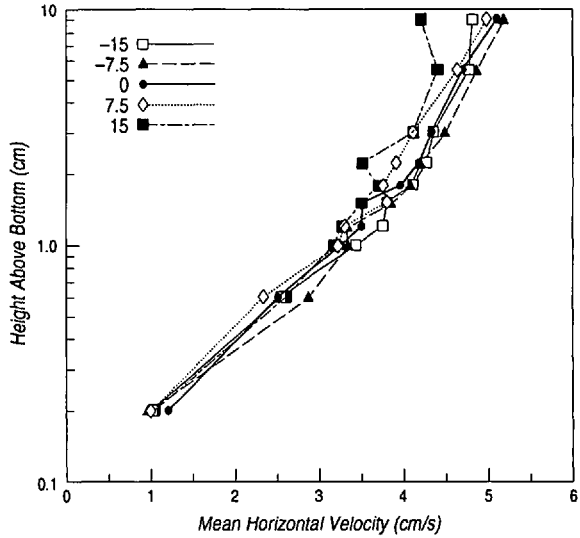

Figure A.2. Cross-channel variation in mean horizontal velocity in the middle of the array. Numbers indicate distances from the flume centerline, with positive values toward the outside flume wall and negative values toward the inside flume wall.

as fitting parameters, ν of 0.013 cm^2/s (for water temperature of 12°C during profiling) and h of 10 cm.

The fit was excellent for the profile in the middle of the array (center of channel), where the flow was expected to be fully developed (Fig. A.1A), with u_* of 0.26 cm s^{-1}, indicating that the flow behaved according to expectations for classical boundary-layer flow over a hydrodynamically smooth surface. In addition, Π was not significantly different from zero, indicating that there was no wake correction for this flow; the entire profile could be adequately described by the "law of the wall." This agrees with results of Nezu and Rodi (1986) who found that Π depends on a Reynolds number (R_*), defined as hu_*/ν, which increased from zero for $R_* < 500$ to a constant value of ~ 0.2 for $R_* > 2000$; R_* for this Paddle-Wheel-Flume flow was 260.

For velocity profiles 1 m and 2 m upstream of the middle of the array (Fig. A.1B and C), there were slight deviations of the points from the curve for fully-developed flow (i.e., Fig. A.1A), indicating that the boundary layer was still growing. Most of the points that deviated from the curve fell to its right, possibly due to weak secondary (cross-stream) flow upstream of the array.

Cross-stream profiles in the middle of the array indicated slight deviations from one-dimensional flow within 10 cm of the flume wall, as indicated by the decreased near-surface velocities in the profiles 15 cm to either side of the flume centerline (Fig. A.2). Flow profiles within the central 15 cm of the flume were similar to each

other and behaved according to classical results, indicating uniform flow across this portion of the channel.

In summary, the array was positioned at a downstream location and within the central region of flow that was fully developed and essentially one-dimensional.

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