Larval settlement in flocculated particulates

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ABSTRACT

Planktonic larval settlement can be a major determinant of population and community dynamics. Settlement templates of benthic invertebrates have been attributed to biological, chemical, and hydrodynamic mechanisms. Completely unexplored, however, is the role of patchy, but widespread, flocculated particulates ("floc") that intermittently rest on substrate surfaces. Motivated by observations of very high (of order 10^6 m^{-3}) larval/postlarval densities in floc from a coastal embayment, this study experimentally identified physical and behavioral mechanisms responsible for these associations. In annular-flume studies, sediment cores were mounted flush with the channel bottom, serving as the floc source. Larval (*Capitella* sp. I, a polychaete worm) distributions in the flume were consistent with predictions for transported particulates. Floc and larvae accumulated at the channel inner corner in high flows (shear velocities, u_*, of 0.8 and 1.6 cm s^{-1}), but not in low flows (u_* of 0, 0.2 and 0.4 cm s^{-1}). Inner-corner concentrations of larvae/floc resulted from a predictable, cross-channel, bottom flow in that direction. In still-water behavioral assays, there were no significant differences in percent metamorphosis among flocs fabricated from particulate-laden seawater, conspecific fecal pellets (compact floc) and organic-rich sediment. Surficial aggregates clearly were acceptable settlement substratum.

This study is the first to show that settling larvae associate with surficial aggregates via both physical and behavioral mechanisms. Floc may be a transient larval venue facilitating habitat search, providing nutrition, or offering protection from predators. Alternatively, it could confer high mortality, reducing larval flux to the bed. Associations between larvae and floc do not supersede established mechanisms of habitat selection. They just thicken the plot.

1. Introduction

Most marine invertebrates with complex life cycles colonize the seafloor via an itinerant larval stage. After swimming or sinking to the bottom, some larvae test the substratum and elect to stay or leave. Settlers may encounter drifting aggregates resting on or wafting just

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above the bed. These flocculated particulates ("floc") are comprised of organic and inorganic particulates coalesced into small masses or as loose mixtures. Potentially serving as a way station, benthic aggregates could facilitate larval search of the seafloor, provide nutrition, or serve as a refuge from predators. Conversely, entrainment within a flocculated false bottom may be fatal, reducing the local flux of settlers to the bed. Whether the outcome is positive or negative, substantial settlement in near-bottom floc could significantly alter benthic population dynamics.

High densities of larvae/postlarvae have been measured in aggregates from pelagic and near-bottom environments. Invertebrate larvae, at maximal densities of 10^3 m^{-3}, were found in marine snow (pelagic aggregates) collected 3-5 m below the water surface, at several locations (Shanks and Edmondson, 1990; Shanks and del Carmen, 1997; Shanks and Walters, 1997). Marine snow contained relatively more large, potentially competent (capable of metamorphosis) than small, pre-competent larval polychaetes. Because pelagic aggregates sink much faster than larvae, it was proposed that competent individuals actively enter aggregates and "ride" them to the bottom (Shanks and Edmondson, 1990; Shanks and del Carmen, 1997).

Substantially higher concentrations of larvae/postlarvae were found in surficial aggregated particulates from a coastal embayment (Buzzards Bay, Massachusetts; C. A. Zimmer *et al.*, in preparation). Mean total density of meroplankton was 1.2×10^6 m^{-3} ($\pm 0.3 \times 10^6$ m^{-3}, SEM) for N = 3 sample days (2–5 samples per day) in floc resting on the bed at 14 m depth. Polychaetes were, on average, 10 times more abundant than bivalves or gastropods. Densities of larvae/juveniles in benthic aggregates were concentrated by about a factor of 100 relative to previously defaunated sediments (trays flush with the bottom) or to near-bottom meroplankton (time-series pump with intake 1 m above bottom; Doherty and Butman, 1990). Tray, pump and floc samples were acquired simultaneously.

Aggregated particulates (marine snow) are created throughout the water column by Brownian motion, shear, and differential sedimentation (McCave, 1984). They sink out of the pelagos and settle on shallow-water to deep-sea bottoms (Alldredge and Silver, 1988). Aggregates are also formed within the bottom-boundary layer, due to large shears and associated mixing (Hill, 1998). Thus, there is a dynamic exchange among particulates resuspended from the bottom and those drifting down from above, creating a mobile pool of near-bottom flocculated particulates (Zimmermann-Timm *et al.*, 1998; Jones *et. al.*, 1998; Cahoon, 1999). These flocs may come to rest on the bed, intermittently, under tranquil conditions (Rhoads, 1973; Roman, 1978; Shimeta *et al.*, 2002). Because they are less dense than the underlying sediment, surficial aggregates are vulnerable to transport by even very slow flows (Stolzenbach *et al.,* 1992; Orvain *et al.,* 2003). Also residing on substratum surfaces are much denser aggregates, such as benthic fecal pellets, transported as bedload or suspended load (Taghon *et al.,* 1984; Andersen and Pejrup, 2002).

Benthic aggregates are compositionally diverse and vary among sites and seasons. Common constituents include mineral grains, organic and inorganic particulates and phytoplankton from the water column (Whitlatch, 1981; Krank and Milligan, 1992; Hill, 1998); particulates and phytodetritus from the bottom (Beaulieu, 2002); and transparent exopolymer particles (TEP) "glue" – sticky mucopolysaccharides released by phytoplankton, bacteria and suspension-feeding bivalves (Alldredge *et al.*, 1993; Heinonen *et al.,* 2007). Floc size and sinking velocity are controlled by particulate composition and concentration, and turbulent mixing (Milligan and Hill, 1998; Fugate and Friedrichs, 2003). As in pelagic aggregates, elevated levels of organic carbon and nitrogen in floc are likely to support rich microbial communities and chemical gradients that drive decomposition and nutrient regeneration (Azam, 1998; Simon *et al.,* 2002). This labile organic pool is readily consumed by benthic invertebrates (Bricelj and Malouf, 1984), and can determine spatio-temporal patterns of species distributions (Kelaher and Levinton, 2003). Thus, benthic aggregates offer settling larvae a physical particulate matrix, particulate organic matter, sticky surfaces and microbial prey.

We studied the mechanistic basis for associations between larvae and floc. Interactions were explored in flume and behavioral experiments. The three-dimensional flow regime in an annular flume transports and localizes particulates to a specific region of the channel. Comparisons between larval and floc distributions revealed the role of passive dispersal and accumulation by physical processes. Complementary still-water studies assessed behavioral and developmental (metamorphic) responses of settlers to aggregates and natural sediments. The collective research addresses the potential role of vagrant near-bottom floc during settlement.

2. Materials and methods

a. Conceptual overview

This research was conducted in two phases. First, annular-flume experiments tested whether larvae accumulate passively in surficial particulates. Second, behavioral assays in still water determined larval metamorphic response to several substrata, including flocs. Flume flows were dynamically scaled to simulate low-energy estuarine and marsh habitats, similar to collection sites used in this study (Signell, 1987; Fingerut *et al.,* 2003). Maintaining fragile field floc in the laboratory for time-sensitive flume trials was intractable. Thus, surficial particulates were gently eroded from the surface of cores filled with organic-rich sediment. Floc is light, accumulates on the sediment surface, and may be transported as bedload or suspended load. To eliminate interactions between cultured larvae and natural infauna, and to distinguish larvae settling in the flume from those previously recruited in field sediment, the organic-rich mud was frozen for 3 d (killing and

disintegrating soft-bodied invertebrates), thawed, and aerated (24 h) before use. The thawed sediment was sieved through a relatively coarse (1 mm) screen to remove large animals and particles that might protrude above the sediment surface, acting as obstacles to the near-bed flow.

Still-water, behavioral assays examined larval responses to surficial aggregates collected in the field, floc fabricated in the laboratory, and conspecific fecal pellets from laboratory cultures. Again, impediments to obtaining natural, intact floc for experiments were insurmountable. Thus, fluffy aggregates were fabricated from particulate-laden near-bottom water.

The source adult population for laboratory-reared larvae was the same for all experiments. Two sediments were used: an east-coast mud for the flume experiments and a west-coast mud for the bioassays. Using organic-rich sediment from marshes on opposite coasts of the United States enabled assessment of a site-specific versus a more generic response of larvae to flocculated particulates, which are innately variable in composition.

b. Study species, larval cultures and competency

Larvae of the polychaete *Capitella* sp. I (Family Capitellidae) were used in all experiments. This species is a head-down deposit feeder that usually lives in muddy sediments rich in organic matter. A classic "boom and bust" opportunist, larvae quickly colonize defaunated, organic-rich sediments, populations grow rapidly, and then steeply decline (Grassle and Grassle, 1974; Chesney and Tenore, 1985). Larvae are lecithotrophic (non-feeding) and competent to settle upon emergence from the maternal brood tube. They can delay metamorphosis for up to 5 d in the absence of an appropriate cue, with no loss in selectivity or decrease in settlement rate (Grassle and Butman, 1989). Upon hatching, larvae initially are phototactic, but become geotactic within 2-3 days, when they swim to the bottom (Butman *et al.,* 1988). In still water and flume flows, larvae preferentially settled in organic-rich muds representative of their natural habitat (Grassle *et al.,* 1992; Thiyagarajan *et al.*, 2005, 2006). Induction of settlement and metamorphosis in *Capitella* sp. I requires direct contact with appropriate substratum; thus far, we have found no evidence of the involvement of a soluble chemical cue (but see Marinelli and Woodin, 2004).

Larvae were raised from stock cultures of out-crossed *Capitella* sp. I adults at 15°C (acclimated to 20°C for experiments) (Grassle and Grassle, 1976; Butman and Grassle, 1992). For annular-flume trials, cultures were reared in Sippewissett Marsh sediment (West Falmouth, Massachusetts, USA; 41°35′30″ W, 70°38′50″ N), which was very high in organic carbon and nitrogen, largely from decaying *Spartina* spp. (Table 1). The sediment surface was free of algal mats. Sippewissett Marsh has long supported *Capitella*

Table 1. Chemical properties of sediments and floc used for rearing adults and in experiments. Because of large, local variation in organic carbon sources at CSMR (Page, 1997), sampling location (middle marsh, boundary, and channel and tidal flat) is critical. Here, bottom sediments and natural floc in near-bed water were collected from the same side of the channel study site.

| Field site | Elemental analysis (%) | | | Stable isotope ratios | |
	Carbon (organic)	Nitrogen	C:N	$\delta^{15}N$	$\delta^{13}C$
Sippewissett Marsh					
Sediment[a]	4.52	0.42	10.8	4.24	−15.72
Carpinteria Salt					
Marsh Reserve					
Sediment[b]	0.92	0.10	9.06	7.07	−19.11
Natural floc[b]	1.73	0.23	7.60	6.57	−20.85
Sediment[c]	1.17	0.12	9.33		
Fabricated floc[c]	1.54	0.20	7.66		

[a]33.4% mud (< 63 μm, silt + clay); bimodal distribution, with major modes in the 20–45 μm (11.0%) and 180–300 μm (30.6%) size classes (Grassle *et al.,* 1992).
[b]These two samples were collected on same day, in same locale.
[c]These two samples were collected on same day, in same locale, but at a different location than the above two samples.

spp. populations (Sanders *et al.,* 1980), and is a common collecting site for *Capitella* sp. I adults.

For behavioral assays, *Capitella* sp. I cultures were raised in sediment collected from a side channel in Carpinteria Salt Marsh Reserve (CSMR), Carpinteria, California, USA (119°31′30″ W, 34°24′16″ N) (Table 1). Mud from CSMR was moderately high in organic carbon. Even though percentages of both C and N were lower in CSMR sediment than in Sippiwissett Marsh sediments, C:N ratios were similar between the two sites. At CSMR, natural floc collected from near-bottom waters contained proportionally more labile nitrogen than organic carbon, resulting in a lower C:N ratio compared to sediment. Epibenthic microalgae were the dominant carbon sources, as indicated by stable isotope ratios for both natural floc and bottom sediment at this site (Page, 1977). There was, however, no evidence of algal mats on the sediment surface or in the floc.

Each run involved a "batch" of larvae, pooled over 48 h from several broods. Prior to an experiment, isolated brood tubes were examined daily, and swimming larvae were collected as they hatched spontaneously. Coincident with a flume trial, three replicate competency tests were conducted in Stender dishes (10 larvae per dish) containing seawater or Sippewissett Marsh mud (methods of Butman and Grassle, 1992). There was no spontaneous metamorphosis in seawater controls, even after 3 h, but all larvae metamorphosed in mud within 15 min of addition.

c. Annular-flume experiments

Flume design and flow characteristics: All flow experiments were conducted in a polycarbonate annular flume (1.5 m diameter, 10-cm-wide channel; Shimeta *et al.*, 2001). It was filled to 10.1-cm depth with 1-μm-filtered seawater. Flow is driven by friction from an annular shear plate floating on the water surface. The plate is rotated by an aluminum drive bar attached, centrally, to a DC motor. Ten circular openings, with removable plugs, are centered 4.1 cm from the inner wall and spaced equidistant around the annulus. Ten cores (3.2-cm inner diameter) fit into the openings and hang below the channel. Core sediment can be extruded level with the flume bed.

Three-dimensional circulation within an annular flume results from the continuously curving channel (Sheng, 1989). The advective along-channel flow generated by the rotating lid experiences a centrifugal force that drives a cross-channel current toward the outer wall at the surface (Fig. 1). To conserve mass, water moves toward the inner wall along the bottom, resulting in a clockwise (facing downstream), three-dimensional helix. If surficial sediments are eroded by the bottom shear stress, they move into the water column via turbulent mixing. Once suspended, particulate transport by the secondary flow is largely a function of the upward flow speed at the inner wall relative to particulate (floc or larval) fall velocity (Fig. 1). In this study, larval and particulate distributions were compared to determine if settlers passively associated with floc.

Flow measurements: Erosion and transport of particulates in the annular flume are determined by floc characteristics and the bed shear stress ($\tau_b = \rho\, u_*^2$, where ρ is fluid density and u_* is shear velocity). At the centerline of each core, τ_b had been measured directly using a calibrated flush-mounted hot-film shear probe (Shimeta *et al.,* 2001), providing flume settings for the u_* used here.
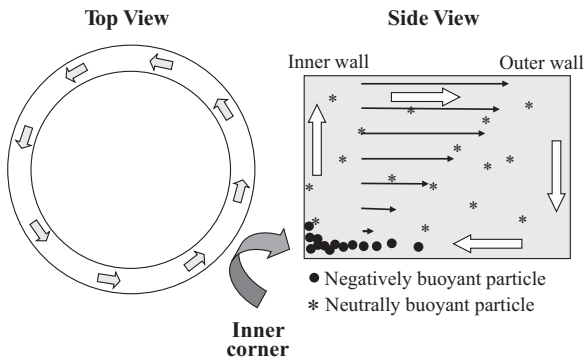

Figure 1. Diagrammatic representation of along- (Top View) and cross-channel flow (Side View) in the annular flume. The bottom boundary-layer flow is indicated by thin black arrows and cross-stream recirculation by larger white arrows.

Annular-flume experiments took place in still water and over the following geometric sequence of u_*: 0.2, 0.4, 0.8, 1.6 cm s^{-1}. The first three values of u_* (0.2, 0.4. and 0.8 cm s^{-1}) bracket those (0.26 and 0.64 cm s^{-1}) used in previous straight-channel flume experiments with *Capitella* sp. I larvae, where particulate transport was nil (Butman and Grassle, 1992; Grassle *et al.,* 1992). In the three-dimensional, annular-flume flows, direct observations of core surfaces showed slight movement of particulates toward the inner corner at u_* of 0.4 cm s^{-1}, and considerable cross-channel particulate transport at u_* of 0.8 and 1.6 cm s^{-1}. Two-dimensional (vertical and cross channel) flow fields were quantified for each u_* using a Dantec 2-axis, backscatter, fiber-optic laser-Doppler velocimeter (LDV).

Experimental protocol: Flume trials tested whether larvae accumulated in the same region of the flume as surficial particulates. Treatments were: (1) **10 cores** of sediment; (2) **1 core** of sediment, location selected randomly for each trial; (3) **no cores** (seawater control); and (4) **floc added** around the inner corner of the no-cores regimen. At least three replicates of each treatment and u_* combination were randomized over time, for a total of 62 runs. Upon completion of a 2-h trial, larvae were quantified in cores (if present), at the inner corner of the flume, and in all water drained from the flume. These three fractions accounted for 92.8% ($\pm$ 0.55% SEM, $N = 62$) of the larvae added.

Based on visual scrutiny of floc movement, passively transported larvae would be expected to accumulate at the inner corner only under high flows (u_* of 0.8 and 1.6 cm s^{-1}) in the 10-core, 1-core, and floc-added treatments. Because more particulates would be eroded from the surfaces of 10 cores versus 1 core, this contrast assessed the effect of inner-corner floc concentration on larval accumulation. The role of larval behavior was evaluated in the flume still-water experiments, where larvae could colonize particulates only by swimming. At a smaller scale, behavioral assays also were conducted in still water (next section).

Basic flume preparation was similar for all experiments. The flume was housed in a 20°C environmental chamber and all runs conducted in the dark. On the day of a trial, aerated mud was added to a core depth of 0.5-0.7 cm, with a several millimeter gap on top. Cores were inserted into the bottom and covered with weighted lids. The channel was filled to 10.1 cm with 1-μm-filtered seawater. Core lids were removed and the mud extruded flush with the flume bottom. Mud surfaces were smoothed, and bottom debris and air bubbles removed prior to a run.

The floc-added treatment was made first conducting a 10-core run (no larvae) at u_* of 0.8 cm s^{-1} for 20 min, during which a substantial amount of particulates accumulated at the inner corner. Flow was stopped, the shear plate removed, and cores covered with weighted lids. Cores were removed and replaced with polycarbonate plugs that fit flush with the flume bottom. The shear plate was re-installed and the flume operated for another 5 min at u_* of 0.8 cm s^{-1} to re-establish natural particulate distributions, with accumulation at the inner corner. The flow (u_*) was set to the experimental value, and larvae were added as described below.

Each flume trial involved a new batch of about 440 larvae (~10 broods), acclimated

to 20°C for at least 24 h. The batch was counted into a beaker 1 h before a run. Once the flume flow had reached terminal velocity, larvae were drawn into a 30-ml syringe connected to tubing protruding through the shear plate. They were gradually discharged below the water surface during one rotation. After a 2-h trial, the plate was removed and each core covered with a lid. Particulates were promptly siphoned from the inner corner using Tygon tubing (3-mm diameter) attached to a 60-ml syringe. Inner-corner collections and flume water were passed, separately, over a 64-μm screen. For the 10-core runs, cores were removed from the bottom in random order. All sample fractions – inner corner, core and water column – were preserved in buffered 80% ethanol, with Rose Bengal stain, sieved (125-μm screen, which retains all larvae) and enumerated. Conspicuous metamorphosis immediately follows settlement and is irreversible.

d. Behavioral assays

The behavioral assays quantified larval metamorphosis in response to five treatments, in separate dishes. One treatment was a seawater control. Three treatments consisted of a single substratum: CSMR mud, CSMR fabricated floc (see below), or aged conspecific fecal pellets (adults feeding on CSMR mud). The fifth treatment was half CSMR mud and half CSMR fabricated floc, testing a substratum preference within a dish. Five replicate dishes of the five treatments were arranged in a Latin-squares design on a table inside a walk-in incubator. There were three replicate runs. Separate preference controls tested whether settlement differed between two sides of a dish filled with the same sediment type. Both halves of the patch were entirely CSMR floc (one experiment) or CSMR mud (another experiment). Each control was performed once, with five replicates.

Substratum treatments were prepared as follows. CSMR mud (top 1 cm) was collected at low tide, and processed as for the Sippewissett sediment: frozen (3 d), thawed, sieved (1-mm screen), and aerated (24 h) before a trial. Aged ($\leq$ 1.5-wk old) fecal pellets were removed from adult cultures. Floc was fabricated from water collected within a few centimeters of the bottom at CSMR and stored at 15°C overnight, allowing suspended particulates to settle. Prior (3 h) to a trial, each carboy was drained to $\sim$ 10-cm depth, and the remaining particulate-laden water poured into two 0.5-liter Nalgene bottles. These bottles were placed on a roller table (Shanks and Edmondson, 1989) and rotated at 1.7 rpm. Loose flocculated aggregates formed within 3 h, due to differential settling (Jackson, 1994). Fabricated floc had similar percentages of C and N, and C:N ratios, as natural floc at CSMR (Table 1).

Larvae and substrata were added to dishes (6.0-cm diameter) filled with 1.5 ml of 0.2-μm filtered seawater. Just prior to a run, a patch (1-cm diameter) of either floc from the roller-table bottles, aged fecal pellets from adult cultures, or mud was placed in the center of a dish. For the preference test, the treatment patch was prepared with mud on one side and floc on the other side of the same dish. Over the course of 5-10 min, 15 larvae were

added just below the water surface of every dish. Trials were run in the dark for 2 h at 15°C. Thus, the addition period was only 4-8% of the experimental interval. Each trial involved a larval batch of at least 3 broods. At the end of a run, all treatments were preserved in buffered 80% ethanol stained with Rose Bengal. The number of metamorphosed (settled) versus unmetamorphosed (swimming) larvae were enumerated.

e. Statistical analyses

Two annular-flume data sets were analyzed statistically: larvae collected in cores (10-core experiment) and larvae accumulating at the inner wall (all experiments). They were tested with a one- (flow) or two-way (experiment by flow) ANOVA, respectively. Number of larvae in the water column was much less variable (within and among treatments) than in cores and at the inner corner. Data from the still-water bioassays were tested statistically using a repeated Latin-squares ANOVA (experiment by treatment) or split plots ANOVAs (preference test and controls). Significant ANOVAs were followed by Tukey-Kramer paired-comparisons tests. Data were arcsine or square-root transformed prior to the ANOVAs, when necessary, to homogenize variances.

3. Results

a. Annular-flume flow

Two-dimensional (cross-stream and vertical) flow fields are presented for flow regimes that regularly (u_* of 1.6 cm s^{-1}) or rarely transported (u_* of 0.4 cm s^{-1}) particulates (Fig. 2). The dominant flow in the annular flume was a large, clockwise circulation cell, as predicted (Sheng, 1989). Vertical velocities on the inner and outer walls were highly asymmetric. A strong, downward jet hugged the outer wall, whereas a wider region of weaker, upward flow transited the inner wall. Likewise, fast flow along the bottom, toward the inner corner, was balanced by much slower return flow throughout the water column. The nucleus of the circulation cell was $\sim$ 1.5 cm above bottom; flow toward the outer wall occupied $\sim$ 85% of the channel depth.

Flume experiments exploited the depositional region at the bottom inner corner of the channel where, at all u_* tested, flow speeds were minimal (Figs. 1, 2). Prior to reaching the inner corner, particulates first must be eroded from the core surface and transported by the near-bed flow. Within millimeters of the bed in the slowest flow (u_* of 0.2 cm s^{-1}), velocities were $\ll$ 0.1 cm s^{-1}, i.e., slower than most larval swim speeds (Butman *et al.,* 1988; Tamburri and Zimmer-Faust, 1996; Krug and Zimmer, 2004). There was no particulate transport in this flow. Near-bed velocities were slightly higher at u_* of 0.4 cm s^{-1} (Fig. 2), and thus, a few particulates moved slowly across the channel and collected at the inner corner. For u_* of 0.8 and 1.6 cm s^{-1}, near-bottom velocities were much higher (2-3 cm s^{-1}) and angled upward. They removed surficial particulates from core surfaces and moved to the inner corner. Moreover, the fastest u_* (1.6 cm s^{-1}) generated sufficient turbulence to mix some particulates away from the walls and into the central flow.
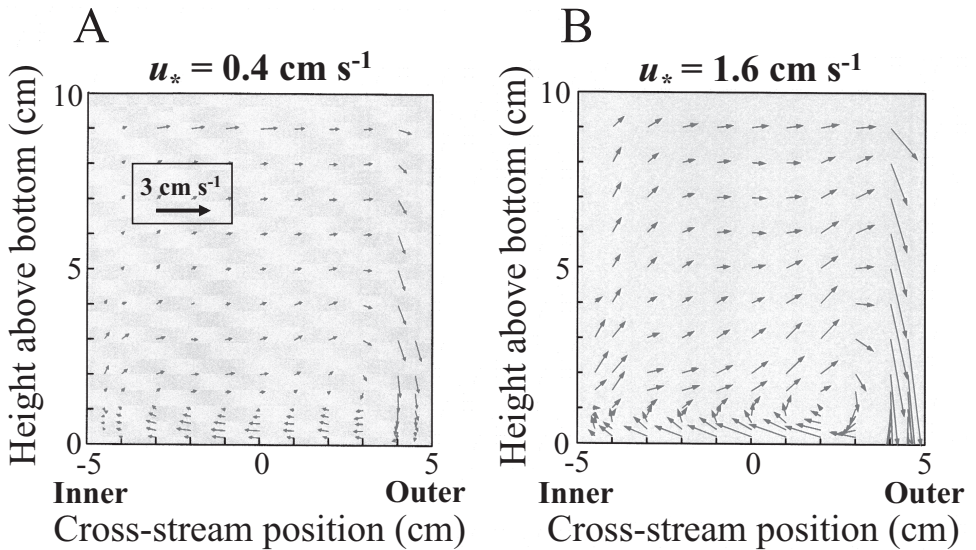
Figure 2. Two-dimensional (vertical, z, and cross-channel, y, directions) flow fields in the annular-flume channel for u_* of 0.4 and 1.6 cm s^{-1}. These two flow regimes are the midpoint and the maximal u_* tested. The fiber-optic probe of the LDV was oriented cross-channel. Bottom and mid-channel were referenced as $z = 0$ and $y = 0$, respectively. Positive y is to the right of the along-channel flow (x dimension). Each arrow is a separate LDV measurement. Arrows are velocity vectors that point in the flow direction, with lengths proportional to flow speed.

b. Annular-flume experiments

To evaluate whether larvae were transported passively like surficial particulates, we focused initially on all fractions of the 10-core treatment, across all flows (Fig. 3). The percentage of larvae in cores decreased with increasing shear velocity. Values were significantly greater in the two slowest flows – still water (78.1%) and u_* of 0.2 cm s^{-1} (69.2%) – than in the three fastest u_* of 0.4 cm s^{-1} (46.6%), 0.8 cm s^{-1} (15.8%) and 1.6 cm s^{-1} (10.3%) (Table 2). Settlement at the intermediate u_* (0.4 cm s^{-1}) was significantly less than at u_* of 0.8 cm s^{-1} and 1.6 cm s^{-1}.

Larvae transported from cores at high u_* accumulated at the inner corner (Fig. 3, Table 3). Significantly fewer larvae were collected at the inner corner in still water (3.7%) than at u_* of 0.4 cm s^{-1} (36.2%), 0.8 cm s^{-1} (73.1%) and 1.6 cm s^{-1} (63.2%). Relationships between flow and percentage of larvae in cores, and flow and percentage of larvae at the inner corner, were nearly mirror images. Combined, the mean percentages of larvae in cores and at the inner corner for each flow accounted for $82.0 \pm 2.5\%$ (SEM, $N = 5$) of the larvae added to the flume. The remainder was recovered from the drained water (mean of $16.4 \pm 1.8\%$ SEM, $N = 5$). In the 10-cores
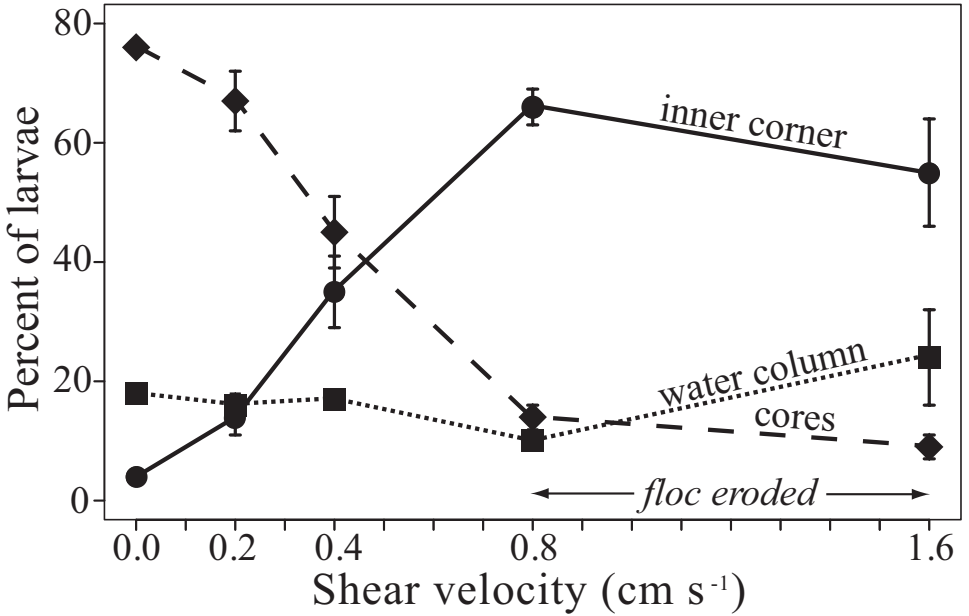
10-Cores Experiment

Figure 3. Mean ($\pm$ 1 SEM) percentage of total *Capitella* sp. I larvae recovered in the 10-Core Experiments. Three fractions – cores, inner corner and water column – were sampled at the conclusion of each run. At least three replicate runs were conducted in still water and for each of the four shear velocities. Continuous and heavy floc erosion from cores was observed at u_* of 0.8 and 1.6 cm s^{-1}, as indicated on the graph. Occasional and light floc erosion occurred at u_* of 0.4 cm s^{-1}. Statistical analysis of the core results is provided in Table 2 and of the inner core results in Table 3. To avoid confusion, significant effects from post hoc comparisons are not shown on the figure.

Table 2. Statistical analysis of the effect of u_* on settlement in the 10-core experiments (Fig. 3). A one-way ANOVA tested whether the mean proportion of settled larvae (in cores/total recovered) collected in the 10-core trials differed among flows (u_*) and still water. Data were arcsine transformed to homogenize variances. The highly significant ($F_{4,11} = 58.078$, $p \leq 0.0001$) ANOVA was followed by a Tukey-Kramer paired-comparisons test (below). Horizontal lines connect means that are not significantly different.

	Flow (u_*, cm s^{-1})				
	0.0	0.2	0.4	0.8	1.6
Mean	0.781	0.692	0.466	0.158	0.103
SEM	0.015	0.053	0.070	0.021	0.025

Table 3. Statistical analysis (two-way ANOVA) of the mean proportion of larvae (number at inner corner/total recovered) collected at the inner corner for all flows (u_*) and experiment types (N = 3, except N = 4 for u_* of 0.8 cm s^{-1} in a 10-core experiment and u_* of 1.6 cm s^{-1} in a 0-core experiment) (Figs. 3 and 4). Data were square-root transformed, prior to the analysis, in order to homogenize variances. Experiment type, Flow, and their interaction, all were highly significant (top). A Tukey-Kramer multiple-comparisons test determined which treatments differed significantly from each other (bottom). In the vertical, **A** or **B** indicate means that are not significantly different among experiment types. For each experiment type, horizontal lines below the means connect values that are not significantly different among flows.

Source	SS	df	F	p
Exp type	1.35	3	35.70	0.00001
Flow (u_*)	0.72	4	14.23	0.00001
Exp type × Flow (u_*)	0.65	12	4.30	0.00198
Error	0.53	42		

| | Flow (u_*, cm s^{-1}) | | | | |
	0.0	**0.2**	**0.4**	**0.8**	**1.6**
Experiment Type					
0 Core					
Mean	0.098 **B**	0.241 **AB**	0.338 **A**	0.182 **B**	0.082 **B**
SEM	0.015	0.112	0.067	0.053	0.027
1 Core					
Mean	0.124 **AB**	0.185 **B**	0.351 **A**	0.355 **AB**	0.261 **AB**
SEM	0.032	0.033	0.135	0.089	0.076
10 Core					
Mean	0.037 **B**	0.141 **B**	0.362 **A**	0.731 **A**	0.632 **A**
SEM	0.001	0.034	0.062	0.032	0.109
Floc added					
Mean	0.473 **A**	0.599 **A**	0.761 **A**	0.764 **A**	0.680 **A**
SEM	0.070	0.054	0.044	0.143	0.087

trials, a mean of only 1.6% of the larvae were unaccounted for. Compared to the cores and inner corner, percentage of larvae in the water was relatively invariant over u_* of 0 to 0.8 cm s^{-1}. At u_* of 1.6 cm s^{-1}, however, the percentage of larvae in the water increased to a mean of 23.7 ± 8.1% (SEM, N = 3), probably because enhanced mixing transported larvae into the water column (see Fig. 2B). Results of the 10-cores trials
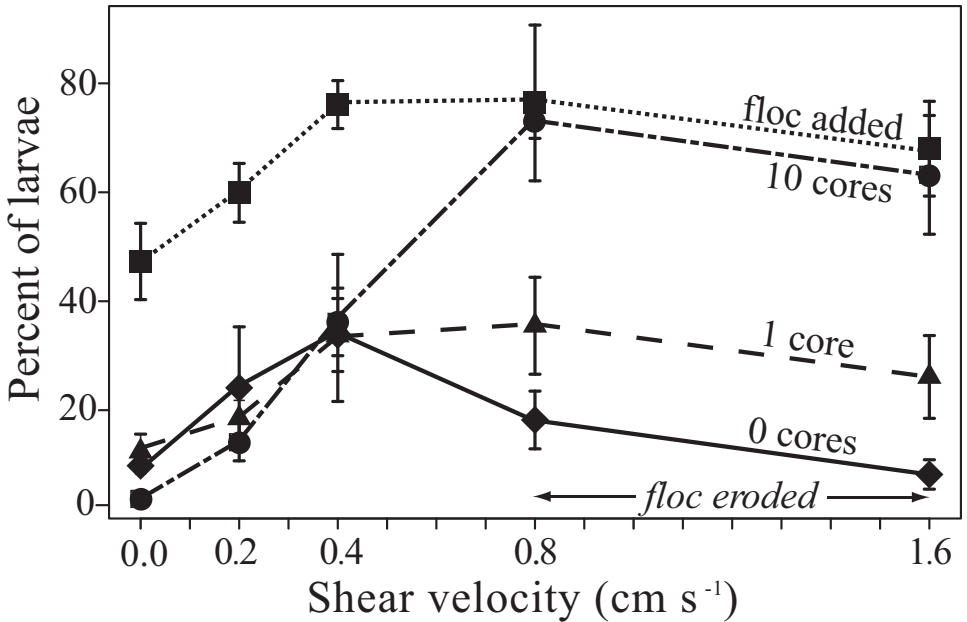
Larvae at the Inner Corner

Figure 4. Mean ($\pm$ 1 SEM) percentage of total *Capitella* sp. I larvae recovered at the inner corner for four types of annular-flume experiments — 0 cores, 1 core, 10 cores and floc added (0 cores) at five flow conditions (0, 0.2, 0.4, 0.8 and 1.6 cm s^{-1}). At least three replicate runs were conducted for each treatment and flow combination. Values at $u_* = 0$ are slightly offset to the right of the vertical axis, for clarity. Continuous and heavy floc erosion from cores was observed at u_* of 0.8 and 1.6 cm s^{-1}, as indicated on the graph. Occasional and light floc erosion occurred at u_* of 0.4 cm s^{-1}. Statistical analysis of the results is provided in Table 3. To avoid confusion, significant effects from post hoc comparisons are not shown on the figure.

support passive larval movement toward, and retention at, the inner corner under flow conditions that transport surficial particulates.

This pattern – larvae and floc accumulating at the inner corner at high u_* – was not statistically significant for any other treatment (Fig. 4, Table 3). In most cases, trends were similar to those in the 10-cores treatment, but were not significant due to low replication (N = 3 or 4). In the floc-added treatment, the inner corner retained high numbers of larvae in all flows, with lower percentages at lower u_*. With or without sediment to generate floc (i.e., the 0-, 1- and 10-core treatments), there was almost the same linear relationship between percentage of larvae at the inner corner and flow, for $u_* \leq 0.4$ cm s^{-1}. The three curves deviated from one another at high u_* (0.8 and 1.6 cm s^{-1}). Floc generated by 1 and 10 cores retained 2-3 and 4-8 times, respectively, more larvae at the inner corner relative to no cores. Thus, inner-corner larvae are associated with floc.
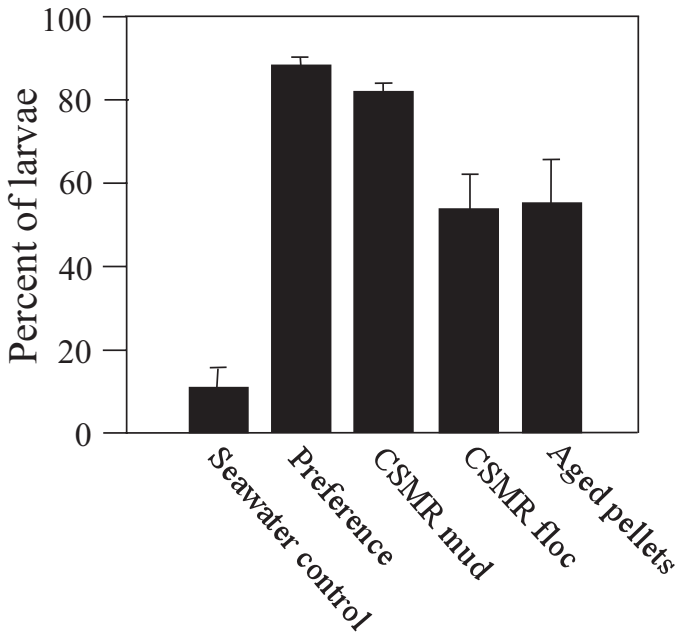
Figure 5. Mean (± 1 SEM) percentage of larvae (*Capitella* sp. I) metamorphosing in response to four different substrates, or a seawater control, offered in small dishes of still water. Three single-substrate treatments were CSMR mud, floc fabricated from near-bottom water collected at CSMR, and aged conspecific fecal pellets from adult cultures (raised on CSMR mud). The last treatment was a two-choice preference test in which larvae were offered, simultaneously, CSMR mud and CSMR fabricated floc, each covering half of the treatment area. Plotted are the grand means for three replicate experiments. Statistical analysis of the results is provided in Tables 4 and 5. Because of the significant Exp X Treat interaction (Table 4), significant effects differ for each experiment, and thus, were not shown on the figure.

c. Behavioral assays

In the behavioral assays, settlement in floc and mud, and pellets and mud, were not significantly different in two comparisons (1 and 3, and 2 and 3, respectively) (Fig. 5, Table 4). The percentage of metamorphosed larvae varied significantly among the five treatments, and post hoc paired comparisons differed among experiments. Settlement was lowest in the seawater control, where all larvae were swimming at the end of the trials. In the other treatments, most larvae settled within 10 min. Highest settlement occurred in the preference test, then the mud, followed by the pellet and floc. The latter two treatments did not differ significantly from each other in all three replicate runs. Larval settlement on the two types of surficial aggregates was not significantly different from settlement in natural CSMR mud.

When given a choice, larvae slightly preferred mud over floc (Table 5). Both the

Table 4. Statistical analyses of the still-water bioassays (Fig. 5). Repeated Latin squares ANOVA, showing significant treatment and experiment by treatment effects. Tukey-Kramer posthoc test for significant main effects; horizontal lines connect treatment means that are not significantly different. *Preference treatment was a choice between CSMR mud and CSMR floc.

A

Source	SS	df	F	p
Experiment	15.39	2	2.09	0.138
Treatment	1360.99	4	92.51	0.001
Row	13.65	4	0.93	0.459
Column	8.72	4	0.60	0.670
Exp × Treat	29.01	8	4.38	0.001
Exp × Row	33.15	8	1.14	0.369
Exp × Column	14.08	8	0.48	0.863
Error	132.40	36		

B

Experiment   **Treatment**

		Seawater control	Aged pellets	CSMR floc	CSMR mud	Preference*
1	Mean	0.0	5.2	9.4	2.0	14.4
	SEM	0.0	0.58	1.08	1.05	0.51

		Seawater control	CSMR floc	Aged pellets	CSMR mud	Preference*
2	Mean	3.0	5.8	8.8	13.0	14.2
	SEM	0.32	1.16	1.16	0.71	0.37

		Seawater control	CSMR floc	Aged pellets	CSMR mud	Preference*
3	Mean	2.0	8.8	10.6	11.4	13.6
	SEM	0.32	1.46	0.68	0.93	0.51

sediment and experiment by sediment interactions were significant, but only one experiment had significantly more settlers in mud than floc (prior contrasts test, $F_{1,4} = 38.83$, $p = 0.001$). Control experiments showed no significant bias of larvae for one side, or the other, of a patch (Table 5).

Table 5. Statistical analyses of the preference treatment and controls in the still-water bioassays. Top: Split plots ANOVA for preference treatment (CSMR mud versus CSMR floc, see text), with experiment as the whole plot factor and sediment and replicate dish as subplot factors nested within experiment. Bottom: Split plots ANOVA for controls (CSMR mud versus CSMR mud, and CSMR floc versus CSMR floc), showing no significant effects of sediment, side of dish, replicate (5 dishes) nested within sediment, or the interactions.

Split plots ANOVA for preference treatment

Source	SS	df	F	p
Experiment	0.87	2	0.79	0.477
Sediment	40.83	1	7.49	0.018
Exp × Sed	177.27	2	16.26	0.000
Rep (Exp)	6.60	12	0.10	0.999
Error	65.40	12		

Split plots ANOVA for controls

Source	SS	df	F	p
Sediment	3.2	1	0.71	0.42
Side	0.2	1	0.04	0.84
Sed × Side	1.8	1	0.40	0.54
Rep (Sed)	36.0	8	1.00	0.50
Error	36.0	8		

4. Discussion

a. Larvae colonize floc

Surficial aggregates are a distinctive feature of low-energy environments, such as bays, estuaries and the deep sea. Often no more than millimeters thick, floc settles onto hard and soft substrata and is compositionally diverse. Moreover, it tends to be patchily distributed and ephemeral due to the transient nature of the generating processes (e.g., turbulent mixing, phytoplankton blooms, particulate supply). Despite these sources of variation, very high invertebrate larval/postlarval densities were measured in surficial floc collected over a several week field study in a shallow, coastal embayment (C.A. Zimmer *et al.*, in preparation).

This study is the first to show that physical and biological mechanisms can associate larvae of a common, mud-dwelling polychaete with surficial aggregates. Flume experiments simulated, to first order, near-bed mixing in estuarine and marsh environments, and thus, results may be relevant to other infaunal species living in such habitats. Positioned between the plankton and the benthos, floc could function as an intermediate step in the settlement process.

Capitella sp. I larvae passively or actively entered floc, and remained there, alive, during the 2-h experiments. Their still-water metamorphic rate was similar in experimental floc treatments and natural mud, indicating that aggregates were acceptable settlement substratum. Larvae readily colonized floc from both east- (flume experiments) and west-

(still-water bioassays) coast organic-rich sediments, suggesting that the response is not peculiar to a particular substratum.

b. How larvae colonize floc

When floc covers a substantial portion of the seafloor, it presents a large target for settlers. Colonization of much smaller floc patches is potentially more interesting. Our experiments showed that larvae passively collided with, and actively swam into, floc. Laboratory scales are difficult to extrapolate directly to the field, but these results suggest that if floc is sufficiently close to *Capitella* sp. I larvae, they are likely to enter it. The three-dimensional annular-flume circulation roughly simulated variations in near-bed hydrodynamics occurring at the scale of settling larvae in the field. Natural bottom topography (e.g., ripples, depressions, shell hash, and cobble) would block, decelerate, accelerate and turn the flow, redistributing particulates and settlers (Snelgrove, 1994; Hines *et al.*, 1997). Thus, feature-induced, small-scale flow patterns may bring larvae into contact with surficial aggregates.

Including floc as a variable in the settlement process does not supersede other established mechanisms of habitat selection. Surficial aggregates are unlikely to interfere with perception and response of suspended larvae to dissolved cues in the water column (Zimmer-Faust and Tamburri, 1994; Swanson *et al.*, 2004). Potential settlers would still encounter floc as they get very close to the seafloor. Like larvae that hit bottom, those individuals touching down on floc may choose to remain there or leave (see Section 3c. *Why larvae colonize floc*). Aggregates transporting like bedload take long or short hops along the bed. At touchdown, colonists contained within the floc may respond to any number of biological, chemical and substratum cues in order to select (Snelgrove and Butman, 1994; Zimmer and Butman, 2000) or reject (Woodin *et al.*, 1993; Marinelli and Woodin, 2004) a settlement site.

Post-settlement redistribution of larvae may inherently involve the physically vulnerable surficial floc layer. Over half of the animals collected in field floc were metamorphosed juveniles. Dispersal by post-settled bivalves has been attributed to both physical and biological processes (Roegner *et al.*, 1995; Hunt, 2004). Susceptibility to erosion depends on substratum type, and floc generally is much easier to erode than underlying sediments. Upward burrowing behaviors would ultimately position juveniles within surficial sediment, or floc, facilitating resuspension and transport (Lundquist *et al.*, 2004; Hunt, 2005).

c. Why larvae colonize floc

As a temporary larval habitat, floc may offer improved substratum selection, enhanced food resources, and protection from predators. Here, behavioral responses of *Capitella* sp. I larvae to surficial aggregates were rapid ($\leq$ 10 min) and consistent. If adaptive, larval residency in floc would be expected, on average, to enhance recruitment success.

Surficial aggregates may facilitate habitat selection for detained individuals. Once larvae enter floc, they would be transported with it. They are unlikely, however, to seek out

flocculated particulates for the specific purpose of dispersal. When unsteady (e.g., tidal) flows drop to very low or no values, floc would deposit on the bed. Following touchdown, potential settlers may vacate aggregates and test the site for acceptability. In most flows, floc would horizontally transport larvae faster than larvae can swim (of order 0.1 cm s^{-1}; Butman *et al.*, 1988; Tamburri and Zimmer-Faust, 1996), saving settlers both time and energy. Likewise, sinking marine snow has been implicated in the vertical transport of associated larvae (Shanks and Edmondson, 1990; Shanks and del Carmen, 1997; Shanks and Walters, 1997).

As a source of nutrition, components of floc may feed planktotropic (feeding) larvae or postlarvae. Food resources limit survival of planktotrophs (Fenaux *et al.*, 1994; McEdward and Miner, 2003). Early nutrition of settlers can determine size at and timing of metamorphosis (Howard and Hentschel, 2005; Emlet and Sadro, 2006), and is a major recruitment bottleneck for juveniles (Jumars *et al.*, 1990; Hentschel, 1998). Like marine snow, floc is rich in organic compounds and phytodetritus (Beaulieu, 2002). Planktonic diatoms that settle in mass aggregations (Alldredge and Gotschalk, 1989), as well as benthic diatoms, may carpet the seafloor (MacIntyre *et al.***;** 1996; Cahoon, 1999). Nutritionally rich, diatoms are a critical food source for small deposit feeders, including *Capitella* sp. I (Marsh *et al.*, 1989; Hentschel and Jumars, 1994).

Floc may protect larvae from visual predators. Planktivorous fish, in particular, limit distributions and abundances of invertebrate larvae (Gaines and Roughgarden, 1987; Ólafsson *et al.*, 1994; Morgan, 1990; Morgan and Christy, 1997). In fact, transparency in planktonic invertebrates, including most larvae, probably evolved in response to visual predators (Johnsen, 2001). Fish exploit available light, from ultraviolet radiation in shallow water ($\leq$ 100 m depth) (Losey *et al.*, 1999) to bioluminescence in the deep sea (Warrant and Locket, 2004). Floc is likely to be more abundant under turbid conditions that discourage prey detection (Utne-Palm, 2002). Surficial aggregations of particulates thus may shelter larvae from their visual predators.

An alternative to adaptive scenarios is that larval entrainment in benthic aggregates is fatal. Given the inherently sticky (e.g., due to TEP) nature of floc, it may subdue, rather than support settlers. Some fish use taste or olfaction to locate high-organic aggregates (Alldredge and Silver, 1988; Larson and Shanks, 1996), consuming the larvae within. Moreover, near-bed aggregates containing larvae are vulnerable to ingestion by benthic suspension- and deposit-feeding invertebrates (Lopez and Levinton, 1987; Shimeta and Jumars, 1991). Live larvae trapped in bivalve pseudofeces, for example, could not escape and died (Tamburri and Zimmer-Faust, 1996). Time spent in floc also may run down the larval metamorphic clock, with dire consequences (Pechenik, 1990).

d. Outlook

Seawater is dirty. Even "clear" tropical seas are sometimes laden with resuspended phytodetritus and sediment runoff from shore. Likewise, the "tranquil" deep-sea bottom is kicked up by intermittent storms. Temperate coastal waters are the other extreme, with

moderate to very turbid conditions most of the time. Thus, in nature, larvae rarely sink or swim down through the filtered, transparent seawater used in laboratory investigations. Previous studies using particulate-free media in laboratory experiments of settlement processes may be limited, given suspended-particulate conditions in most natural near-bottom waters. In fact, 35+ years of mechanistic studies in a parallel system – holoplankton in marine snow – have shown that a wide diversity of meaningful interactions take place in the very dirty sea.

Larvae reach the seafloor and settle on hospitable substratum through an expanding array of strategies. Hydrodynamic processes passively distribute larvae at a variety of time and space scales. Likewise, larvae behaviorally respond to far more information, biotic and abiotic, than once seemed possible. Most impressive are the interactions. In this vein, floc, suspended signal molecules and benthic cues likely combine to secure a suitable habitat for selective settlers.

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