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Adult macrofauna effects on *Capitella* sp. I larval settlement: A laboratory flume study

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ABSTRACT

The opportunistic, deposit-feeding polychaete *Capitella* sp. I is the overwhelming numerical dominant in disturbed and enriched sediments and rarely co-occurs in appreciable numbers with other abundant mud-dwelling macrofauna. Rapid colonization and population increase in organic-rich sediments is typically followed by subsequent sharp decline. The mechanistic basis for these characteristics was explored in flume-flow experiments that tested whether settling *Capitella* sp. I larvae avoid sediments inhabited by macrofaunal adults or sediments reworked by them. The first set of experiments consisted of four treatments: conspecific adults or no adults in reworked or non-reworked sediment. *Capitella* sp. I settlement was significantly altered (depressed) only by pelletized sediment of conspecific adults. The second set of experiments involved similar treatments, but with adults of the deposit-feeding bivalve *Tellina agilis*. Neither adult presence nor sediment reworking significantly affected settlement of *Capitella* sp. I larvae. A third set of experiments that compared settlement in sediments with and without the suspension-feeding bivalve *Mulinia lateralis* demonstrated no significant treatment effect. These results suggest that larval settlement behavior could contribute to population growth in a “boom and bust” species when a critical limiting resource is overexploited. That is, sediments completely pelletized by *Capitella* sp. I adults may signal settling larvae that organic matter is depleted. Larvae may therefore settle in smaller numbers and are more likely to be dispersed away from abundant populations of adults. Active avoidance of conspecific adults or adults of other taxa is unimportant for the taxa at the densities tested here.

1. Introduction

Opportunistic, deposit-feeding polychaetes in the genus *Capitella* characteristically reach high abundances in organically enriched sediments. Such habitats typically occur in estuarine and coastal areas impacted by organic and inorganic pollutants, and thus dense populations of *Capitella* spp. are considered “pollution indicators” (e.g. Pearson and

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Rosenberg, 1978; Chang *et al.*, 1992; Lenihan and Oliver, 1995). To understand the specific aspects of a polluted environment that are indicated by the presence of *Capitella* spp. requires fundamental knowledge of their basic ecology. Morphological similarity among adults and geographical co-occurrence of species and sibling species within the genus *Capitella* and related genera (Grassle and Grassle, 1974; 1976; Grassle *et al.*, 1987), render it difficult to conduct extensive experimental manipulations in the field. Experiments under simulated natural flow conditions in laboratory flumes, however, have yielded meaningful ecological insights for the easily cultured *Capitella* sp. I (e.g. Butman *et al.*, 1988a; Grassle *et al.*, 1992a).

Capitella sp. I, a head-down deposit-feeder, is strongly associated with organic-rich sediments. It is the most geographically widespread of the *Capitella* species, and has a classical opportunistic life history—rapid colonization and population increase followed by subsequent sharp decline (e.g. Grassle and Grassle, 1974; Chesney and Tenore, 1985). It is typically the overwhelming numerical dominant and thus rarely co-occurs in appreciable numbers with other abundant infaunal organisms. Most previous studies have focused on input of organic matter as a factor that may be responsible for population distributions and dynamics of *Capitella* sp. I. In terms of larval settlement, research emphasis has been on the role of sediment characteristics, particularly organic carbon content (e.g. Grassle *et al.*, 1992a; Cohen and Pechenik, 1999), and the near-bed flow regime (e.g. Butman and Grassle, 1992; Snelgrove *et al.*, 1993). In contrast, this study addresses interactions between settling *Capitella* sp. I larvae and conspecific adults, adults of other macrofaunal species, and sediments reworked by conspecific and other adults.

Capitella sp. I larvae are lecithotrophic and competent to settle upon release from the brood tube, they select organic-rich over organic-poor sediments in both still water and flume flow, and this selectivity is maintained over 3–6 days in the absence of a sediment cue (Butman *et al.*, 1988a; Butman and Grassle, 1992; Grassle *et al.*, 1992a). Induction of settlement and metamorphosis appears to require direct contact between larvae and sediment. Moreover, settlement patterns can be modified by interactions between the near-bottom flow and larval behavior (Snelgrove *et al.*, 1993). Upon release from the brood tube, larvae are positively phototactic (Butman *et al.*, 1988b) and susceptible to even weak turbulence that transports them away from (Grassle *et al.*, 1992b) or toward (Snelgrove *et al.*, 1993) the bed. These characteristics have the potential to facilitate dispersal of *Capitella* sp. I larvae from the natal habitat. Their capacity to postpone metamorphosis in the absence of a suitable cue may improve the probability of ultimately settling in hospitable habitat, where there is enhanced growth and survival.

Studies of the mechanisms responsible for the “boom and bust” population dynamics of *Capitella* sp. I suggest that colonization and subsequent population increases depend on the availability of small, “labile,” organic particles that are nitrogen-rich (e.g. Grassle and Grassle, 1974; Phillips and Tenore, 1984; Tenore *et al.*, 1984; Chesney and Tenore, 1985; Hornig and Taghon, 1999). These particles, having passed once through a worm gut and packaged into fecal pellets, may have a reduced capacity to support individual or

population growth. Indeed, *Capitella* sp. I is very efficient at decomposing organic matter, and has been used in bioremediation—for the treatment of organic-polluted sediments underlying fish farms in marine net pens (e.g. Tsutsumi, 1990; Chareonpanich *et al.*, 1994). Continuous inputs of organic matter are required to sustain high densities of *Capitella* sp. I (e.g. Holte and Oug, 1996). Over-exploitation of food resources by *Capitella* sp. I populations that have exceeded carrying capacity can contribute to large population oscillations (e.g. Chesney and Tenore, 1985).

The responses of *Capitella* sp. I larvae to sediment conditions could contribute to both the steep rise and the precipitous fall in *Capitella* sp. I populations. Larvae clearly select high-organic sediments at settlement, but they also do not co-occur in high abundance with established populations of other deposit or suspension feeders (e.g. Grassle and Grassle, 1974; Ambrose, 1984; Elmgren *et al.*, 1986; Hunt *et al.*, 1987). Once established, fast population growth could be facilitated by some lecithotrophic larvae of *Capitella* sp. I that metamorphose within the maternal brood tube, by-passing the planktonic stage and crawling to surrounding high-organic sediments (authors' pers. obs).

As the population grows, settlement may be reduced or arrested via disturbance (e.g. Woodin *et al.*, 1998) by conspecifics, although this possibility is unlikely, given that *Capitella* sp. I is a head-down, subsurface, deposit feeder and adult feeding activities only minimally affect the sediment-water interface. Settling larvae may be deterred by high concentrations of chemical-defense compounds, such as halogenated metabolites, in *Capitella* sp. I tissues (e.g. Woodin *et al.*, 1997). However, because pre-release larvae harbor even higher concentrations of haloaromatics than their parents (Coward *et al.*, 2000), it is not clear who would be defending against whom. Finally, in dense *Capitella* sp. I populations, the surface sediment consists almost entirely of fecal pellets. Given that sediment selection by *Capitella* sp. I larvae clearly depends on the quality and quantity of sedimentary organic matter (Grassle *et al.*, 1992a), pelletized sediment, from which much of the labile organic pool has been removed during gut passage, should be distinctly unattractive to settlers. Moreover, a considerable portion of the protein in sediments is difficult to hydrolyze, and therefore of less use to deposit feeders (Mayer *et al.*, 1995).

This study explores specific mechanisms to explain *Capitella* sp. I population distributions and dynamics—in particular, that *Capitella* sp. I often lives in essentially monospecific macrofaunal communities that develop and grow quickly but eventually crash, and that its occurrence is low in communities containing other abundant mud-dwelling infauna. First, we evaluated the influence of *Capitella* sp. I adults on conspecific larval settlement. Experiments distinguished between effects due to the worms versus due to their sediment reworking activities (ingesting and pelletizing the mud). Second, we evaluated the impact on *Capitella* sp. I settlement of adults of two other infaunal species, the bivalves *Tellina agilis* and *Mulinia lateralis*. *T. agilis* is a surface deposit feeder that could affect settling larvae through its sediment reworking activities, but may also influence settlers through disturbance. The appearance of this species has been known to coincide with declines in *Capitella* spp. populations (e.g. Rhoads *et al.*, 1978). *M. lateralis* is a relatively opportunis-

tic suspension feeder that typically resides in organic-rich sediments similar to *Capitella* sp. I habitat (e.g. Oviatt *et al.*, 1984). Like *Capitella* sp. I, *M. lateralis* larvae select these sediments in flow (Grassle *et al.*, 1992b). *Capitella* sp. I settlement may also be affected by the suspension-feeding activity of *M. lateralis* adults, which may alter flow streamlines (e.g. Monismith *et al.*, 1990) or potentially even ingest larvae (e.g. Tamburri and Zimmer-Faust, 1996).

2. Materials and methods

a. Experimental approach and design

This is an experimental, laboratory-flume study on adult-larval interactions. It does not seek to recreate the precise biological and biogeochemical environments that *Capitella* sp. I larvae might encounter in nature. Rather, relevant parameters are varied or controlled in this first step toward identifying biological factors that may influence settlement under simulated natural flow conditions. For larvae known to be highly selective in flow, this study asks whether they make different choices in the presence of infaunal adults (conspecific or otherwise), and, if so, are results due to the presence of the animal per se or to their effects on sediments? Qualitative criteria were used to establish the sediment-reworking interval (several weeks) for obtaining “reworked sediments.” *Capitella* sp. I adults, for example, were allowed to rework mud until the sediment surface was completely pelletized, as would be expected in dense populations in nature. No geochemical measurements were made to match laboratory reworked sediments to those in the field; such comparisons are unlikely to be meaningful given that field sediments contain organisms other than those tested in the laboratory, and that experimental sediment had been frozen, thawed, and sieved. Results are interpreted in view of these experimental constraints.

b. Larval cultures and competency

Larvae were obtained as they hatched from brood tubes of *Capitella* sp. I stock cultures maintained at 15°C. Protocols for adult maintenance and larval handling were described by Grassle and Grassle (1976) and Butman and Grassle (1992). Only broods hatched within ≤ 3 d were used in an experiment and larvae were held at 15°C until several hours before the experiment began. Competency tests similar to those described in previous *Capitella* sp. I studies (e.g. Butman *et al.*, 1988a; Grassle and Butman, 1989) were conducted during all experiments to ensure that larvae were competent and healthy. Briefly, small dishes were filled to 1-cm depth with filtered seawater and a small patch (1 cm diameter) of each of the sediment treatments (described below) was placed in the center of each of three replicate dishes. At the same time, three additional dishes served as filtered seawater controls (i.e., with no sediment added). Five larvae were added to each of the six dishes and examined regularly throughout the simultaneous flume experiment.

c. The flume

Larval choice experiments were conducted in the Paddle-Wheel Flume at the Coastal Research Laboratory of Woods Hole Oceanographic Institution. The flume was described by Butman and Grassle (1992), with modifications described by Snelgrove *et al.* (1993). The steady, recirculating flow is driven by plexiglass panels on a paddle wheel to gently transport planktonic organisms in the flow. The racetrack-shaped flume has a 6.1-m-long straightaway on the side opposite the paddle wheel in which the “test section” is located. As in Snelgrove *et al.* (1993), a panel of the flume bottom between ~3.0 and 4.5 m from the upstream end was replaced with a plexiglass panel containing sixteen uniformly spaced circular compartments in a 4 × 4 array. Each compartment was 3.8 cm in diameter and 2 cm in depth; compartments were farther apart in the downstream direction (~12.6 cm between closest points) than in the cross stream direction (~4.4 cm between closest points) so that flow disturbances created by adult feeding structures or activities would be dissipated before the next downstream treatment. Array width was constrained by wall boundary-layer considerations (e.g. Nowell and Jumars, 1987). Sediment was added to each compartment so that the sediment surface was flush with the floor of the flume. All experiments used “Sippewissett mud,” an organic-rich mud collected from Sippewissett Marsh, West Falmouth, Massachusetts, and the same mud used to maintain the stock *Capitella* sp. I cultures, and in previous sediment choice experiments (Grassle *et al.*, 1992a; Snelgrove *et al.*, 1993). Thus, it is a sediment in which *Capitella* sp. I larvae settle quickly, and in which *Capitella* sp. I adults grow rapidly. Although we do not know that the other adult species tested occur in this particular site, we chose taxa that occur in muddy sediments.

d. Experimental treatments

Three types of experiments were conducted where adults were placed in the flume sediments at natural densities to determine how they affect *Capitella* sp. I larval settlement. Experiments with *Capitella* sp. I adults tested whether larvae respond negatively to the presence of conspecifics. *Tellina agilis* occurs in sandy and muddy habitats from Massachusetts to Georgia, USA (Abbott, 1974) and was chosen because it can be abundant in deposit-feeding mud communities where *Capitella* spp. are relatively rare, and because it is a deposit feeder. *Mulinia lateralis* is a suspension feeder that occurs in mud bottoms from eastern Canada to the West Indies, generally in regions where densities of *Capitella* spp. are low. In fact, in some areas, *M. lateralis* densities increased as *Capitella* spp. densities decreased following an initial disturbance (e.g. Grassle and Grassle, 1974; Rhoads *et al.*, 1978). Thus, in experiments with *T. agilis* and *M. lateralis* adults, the *a priori* prediction is that *Capitella* sp. I larvae will settle in low numbers resulting from disturbance or engulfment of larvae or juveniles, and/or altered sediment quality. Three experiments were run using conspecifics or *Mulinia lateralis* adults, but only two experiments were run using *T. agilis* adults because of problems with larval availability.

i. Capitella sp. I adults. For experiments with adult *Capitella sp. I* (hereafter referred to as “*Capitella* Adult Experiments”), mud collected from the study site was frozen, later sieved over a 1-mm screen and refrozen, and then thawed and treated in one of two ways. For one treatment (“Fresh Mud”), the mud was thawed, mixed well and placed in a large culture bowl in a 15°C incubator prior to filling the appropriate compartments. For the other treatment (“Reworked Mud”), sediment was produced by sieving and combining the fecal pellets produced by ~50 adult *Capitella sp. I* individuals in each of multiple finger bowls in which adults had reworked sediments for ~two weeks prior to use in larval-settlement experiments. Reworking was allowed to proceed until the sediments were completely pelletized, as has been noted in field situations to sediment depths of 15 cm where *Capitella* spp. are abundant (Fleming, 1989; Gallager and Keay, 1989). Fecal pellets were separated from worms and any unpelletized sediment using a 300 µm sieve, and thus, only the pellets were used as the Reworked Mud. The fecal pellets were stored at 4°C until needed. This procedure did not disaggregate *Capitella sp. I* pellets, which are encased in a strong membrane and are notoriously robust (Fleming, 1989; Gallager and Keay, 1989). In addition to these two types of mud (Fresh and Reworked), 10 adult *Capitella sp. I* (1-cm length) were added to eight of the compartments and no adults were added to the other eight. Thus, there were 4 replicates each of 4 treatments (Fresh Mud, Fresh Mud + 10 adults, Reworked Mud, and Reworked Mud + 10 adults), arranged in a Latin squares design.

ii. Tellina Adult Experiments. For experiments with adult *Tellina agilis*, the treatments were similar to those described above. The thawed Sippewissett Mud was either mixed and held at 15°C (“Fresh Mud”) or contained ~6 individuals of *T. agilis* (“Reworked Mud”) that had reworked the mud for ~two weeks. For both treatments, the seawater was decanted off every few days and replaced with fresh seawater. In this instance, the degree of reworking was substantially less than that in the *Capitella* Adult Experiments. Indeed, pelletization was not pronounced. In addition to the two types of mud, one adult *T. agilis* (1-cm length) was added to eight of the compartments and no adults were added to the other eight. As in the *Capitella* Adult Experiments, this resulted in four replicates each of four treatments (Fresh Mud, Fresh Mud + 1 Adult, Reworked Mud, and Reworked Mud + 1 Adult) which were arranged in a Latin square design.

iii. Mulinia Adult Experiments. The final group of experiments involved the suspension feeder *Mulinia lateralis*. Because suspension feeders do not rework sediments to the same extent as deposit feeders, no “Reworked Mud” treatments were tested. For these experiments, one *M. lateralis* adult (2-cm length) was added to each of eight compartments and no adults were added to the other eight compartments, resulting in eight replicates of two treatments (Fresh Mud and Fresh Mud + 1 Adult) arranged in a checkerboard design.

e. Experimental protocol

The day prior to an experiment, compartments of the array were filled with the sediment treatments and covered with weighted caps. The flume was then filled to a depth of 10 cm

with 1- μm -filtered seawater. Once the water level was well above the weighted caps, the caps were removed and sediments were left overnight to equilibrate with the flume water. The following morning, adults of the particular test species were placed on the sediment surface of the appropriate treatments so they could burrow into the sediment while *Capitella* sp. I larvae were being counted under a dissecting microscope. For the *Capitella* Adult Experiments, 10 individuals were distributed as evenly as possible over the surface of appropriate compartments. For the *Tellina* Adult and *Mulinia* Adult Experiments, one individual was placed on the surface at the center of the appropriate compartments. For all experiments, adults were observed for approximately 10 min, and then at 10-min intervals until the experiment began (about 2 h later), to determine whether they migrated to another compartment. None were observed migrating.

Water temperature was $21.4 \pm 1.3^\circ\text{C}$ ($n = 8$), and adults and larvae were acclimated to that temperature for ~ 4 h prior to the start of an experiment. *Capitella* sp. I and *Tellina agilis* adults quickly burrowed into the sediment; siphons of *T. agilis* soon extended above the sediment surface and began deposit feeding, and *Capitella* sp. I tubes were soon seen to extend slightly above the sediment surface. *Mulinia lateralis* adults behaved less consistently; some individuals burrowed into the sediment before beginning to suspension feed, but others began feeding without burrowing into the sediment. These individuals were, therefore, gently nudged into the sediment and observed to be sure that they began feeding again before experiments were initiated.

All experiments were conducted in a slow, turbulent flow with a boundary shear velocity (u_*) of $\sim 0.26 \text{ cm} \cdot \text{s}^{-1}$ (Butman and Grassle, 1992). This flow occurs midway through the tidal cycle in a typical coastal embayment (e.g. range of u_* for tidal flow in Buzzards Bay, Massachusetts is 0 to $0.60 \text{ cm} \cdot \text{s}^{-1}$; Butman, 1986). Horizontal velocity at 7 cm above the bottom was about $5 \text{ cm} \cdot \text{s}^{-1}$.

For each experiment, *Capitella* sp. I larvae were counted into four aliquots of 750 individuals each (3000 total) and added to the flume 1 cm below the water surface in the straightaway 3 and 4 m upstream of the first row of sediment compartments (two aliquots at each point). After 2 h the flow was stopped, weighted caps were placed over the compartments, the flume was drained, and the sediment was carefully removed from each compartment and preserved in 90% ethanol with Rose Bengal stain. This mode of preservation was adequate for these experiments because the identity of the species was known. Samples were enumerated under a dissecting microscope to determine numbers of settled *Capitella* sp. I larvae and the number of adults.

f. Data analysis

All of the experiments were designed to test the null hypothesis that *Capitella* sp. I settlement is not affected by the presence of adults or by their reworked sediments. That is, comparable numbers are expected in each sediment compartment, regardless of whether the sediment was fresh or reworked, and regardless of whether adults were present or absent.

Table 1. Summary of experimental conditions for larval settlement experiments.

Adult taxon	Expt.	Date (day-mo-yr)	Adults added per compartment	Temperature (°C)	Number added	Number larvae recovered in sediments (%)
<i>Capitella</i> sp. I	1	15-05-94	10	20.2	3000	292 (9.7)
	2	16-05-94	10	20.0	3000	226 (7.5)
	3	30-05-94	10	19.0	3000	189 (6.3)
<i>Tellina agilis</i>	1	26-06-94	1	21.8	3000	594 (19.8)
	2	27-06-94	1	21.5	3000	683 (22.8)
<i>Mulinia lateralis</i>	1	28-06-94	1	22.5	3000	368 (12.3)
	2	08-07-94	1	23.0	3000	255 (8.5)
	3	09-07-94	1	20.5	3000	313 (10.4)

Larval settlement patterns were analyzed separately for each of the adult species tested using the ANOVA model $y = \mu + \text{Experiment} + \text{Row} + \text{Column} + \text{Treatment} + \text{Experiment} \times \text{Row} + \text{Experiment} \times \text{Column} + \text{Experiment} \times \text{Treatment} + \text{Error}$, where μ is a constant; Experiment is the replicate experiments, Row and Column are blocking factors to account for spatial location of treatments within the array, and Treatment is the main effect (i.e. testing for differences between Fresh Mud, Fresh Mud with Adults, Reworked Mud, and Reworked Mud with Adults of either *Capitella* sp. I or *T. agilis*, or between Fresh Mud with or without *M. lateralis* adults). Because *F*-tests indicated heteroscedasticity, data were $\log(x + 1)$ transformed to homogenize variances among treatments. When significant differences were observed for any of the main effects, Tukey's HSD Multiple Comparisons tests were performed to determine which means differed significantly.

3. Results

a. Competency

Larvae in the competency test sediments settled and metamorphosed quickly. After 30 min, 90–100% of larvae had settled in Fresh Mud, and 67–100% of larvae had settled in Reworked Mud. In dishes containing seawater and no sediment, <5% of the larvae settled, even after 2 h. These representative data indicate healthy and competent larvae in the flume experiments reported here.

b. *Capitella* Adult Experiments

Experimental temperatures ranged from 19.0–23.0°C ($\bar{x} = 21.4$, $sd = 1.3$; Table 1). Larval recovery ranged from 6.3% to 22.8% of the 3000 larvae originally added in each experiment (Table 1), similar to recovery in previous flume experiments with this species (e.g. Butman *et al.*, 1988a, b; Grassle *et al.*, 1992a). In the *Capitella* sp. I Adult experiments, only one adult *Capitella* sp. I was found in a Reworked Mud treatment (*Capitella* Adult Expt. 3). Within treatments to which adults had been added, there was

Table 2. ANOVA results for settlement of *Capitella* sp. I larvae in treatments with or without *Capitella* sp. I adults in fresh or reworked sediment. Data were $\log(x + 1)$ transformed to homogenize variances. Results from Tukey's comparisons are given below table; means that are not significantly different are joined by lines.

Source	df	SS	F	p
Experiment	2	1.469	5.326	0.015*
Row	3	7.152	39.056	0.000***
Column	3	0.121	0.081	0.968
Treatment	3	2.474	10.122	0.009***
Experiment \times Row	6	0.366	0.443	0.841
Experiment \times Column	6	2.965	3.584	0.016*
Experiment \times Treatment	6	0.489	0.591	0.734
Error	18	2.482		

*** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$.

Fresh sediment + adults	Fresh sediment	Reworked sediment	Reworked sediment + adults
19.08	18.58	11.00	10.25
Row 1	Row 2	Row 3	Row 4
26.17	13.00	11.25	8.50

some variation among compartments; numbers ranged from 9 to 15, except that only 4 individuals were recovered from one of the Fresh Mud + Adult treatments in *Capitella* Adult Expt. 3. This result suggests counting error in addition to migration. For the *Tellina* Adult and *Mulinia* Adult experiments, adults stayed in the appropriate compartments in all cases. In some instances, adults did not feed actively throughout the experiment.

Analysis of variance for the *Capitella* Adult experiments indicated significant Experiment, Row, and Treatment effects (Table 2, Fig. 1). The significant Experiment effect indicates variation in recovery among experiments. Because none of the treatment-related interaction terms was significant, Tukey's comparisons were made by combining the three experiments into a single comparison of 4 means based on 12 replicates. Tukey's tests for the Row effect indicated that significantly more larvae settled in the first (upstream) row than in the three downstream rows, and the second row had significantly higher settlement than the fourth row. Tukey's tests for the Treatment effect indicated significantly higher settlement in the Fresh Mud + Adults than the Reworked Mud + Adults. Fresh Mud alone also had significantly higher settlement than Reworked Mud + Adults. Settlement did not differ between the two Fresh Mud treatments (with or without adults) or between the two Reworked Mud treatments (with or without Adults).

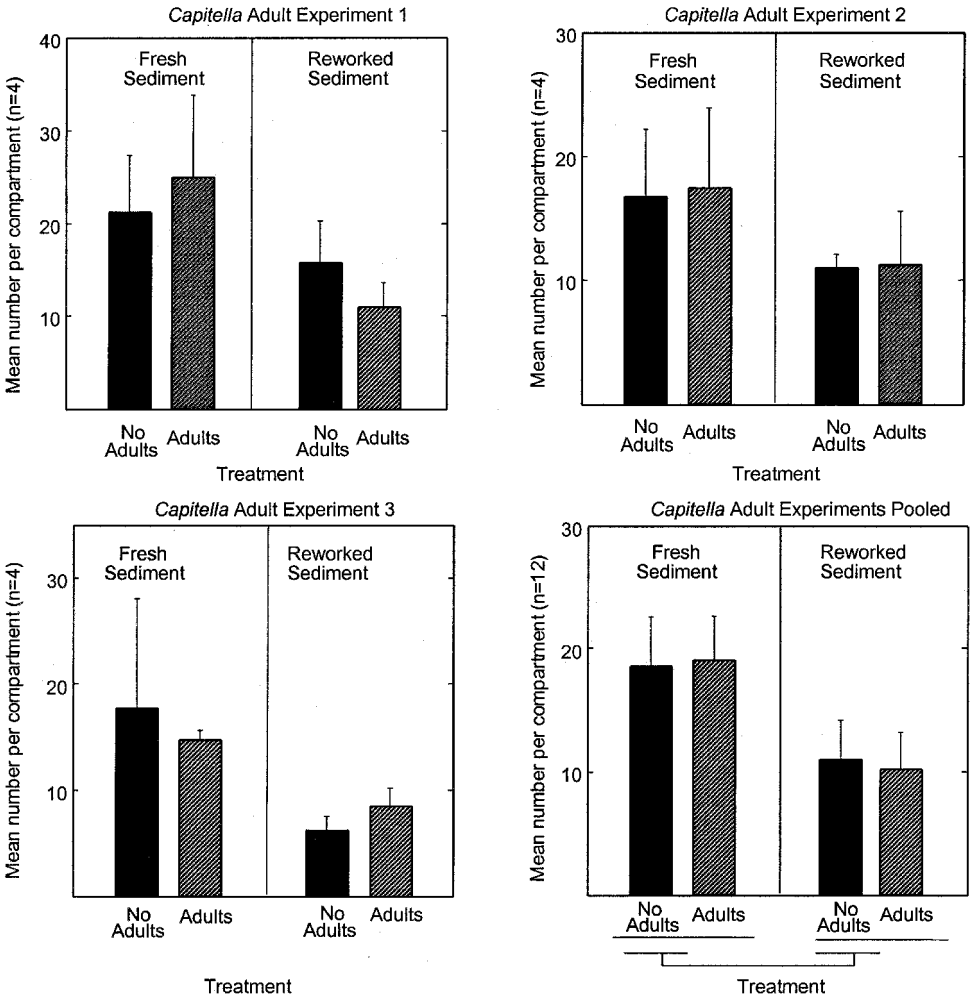


Figure 1. Results from individual experiments and pooled results for experiments with and without *Capitella* sp. I adults present and with reworked versus fresh sediment. Bars denote means ($n = 4$) and lines above bars denote 1 standard error. Lines beneath pooled results join treatments that were not significantly different.

c. *Tellina* Adult Experiments

Analysis of variance for the *Tellina* Adult experiments indicated a significant Column effect (Table 3, Fig. 2). In this case, the Treatment effect was not significant. As above, experiments were pooled resulting in Tukey's comparisons based on 12 replicates of each of 4 treatments. Tukey's tests for the Column effect indicated that significantly fewer individuals settled in Column 1, the column nearest the outside of the flume wall, than in Columns 2 and 4.

Table 3. ANOVA results for settlement of *Capitella* sp. I larvae in treatments with or without *Tellina agilis* adults in fresh or reworked sediment. Data were $\log(x + 1)$ transformed to homogenize variances. Results from Tukey's comparisons are given below table; means that are not significantly different are joined by lines.

Source	df	SS	F	p
Experiment	1	0.023	0.177	0.682
Row	3	0.135	1.054	0.483
Column	3	3.494	60.712	0.003**
Treatment	3	0.210	1.049	0.485
Experiment × Row	3	0.128	0.990	0.430
Experiment × Column	3	0.058	0.446	0.724
Experiment × Treatment	3	0.200	1.552	0.252
Error	12	0.129		

***0.001, **0.01, *0.05.

Column 1	Column 3	Column 2	Column 4
13.50	36.50	48.00	61.62

d. Mulina Adult Experiments

Analysis of variance for the *Mulina* Adult experiments indicated that only the Column effect was significant (Table 4, Fig. 3). Tukey's tests for the Column effect indicated that significantly fewer individuals settled in the column nearest the outside flume wall than in the two innermost columns, and the three inner-most columns were not significantly different.

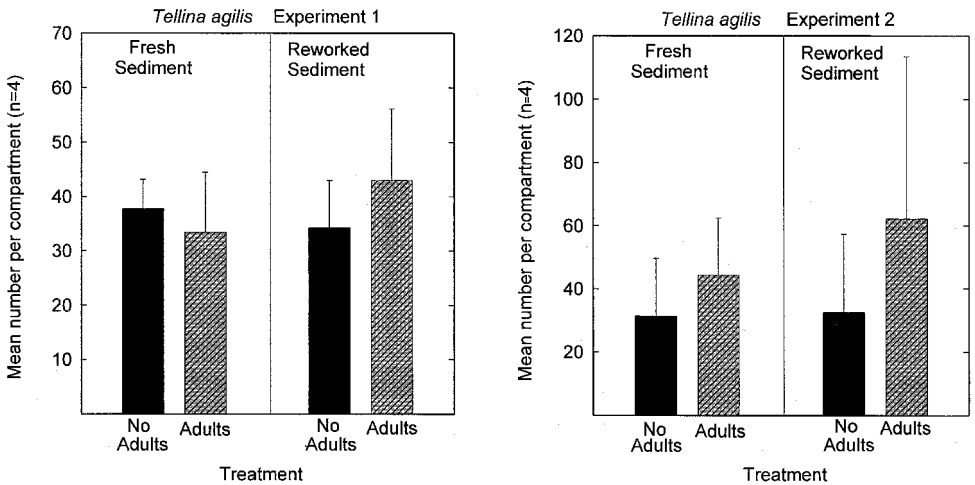


Figure 2. Results from individual experiments with and without *Tellina agilis* adults and with reworked versus fresh sediment treatments. Bars denote means ($n = 4$) and lines above bars denote 1 standard error.

Table 4. ANOVA results for settlement of *Capitella* sp. I larvae in treatments with or without *Mulinia lateralis* adults. Data were $\log(x + 1)$ transformed to homogenize variances. Results from Tukey's comparisons are given below table; means that are not significantly different are joined by lines.

Source	df	SS	F	p
Experiment	2	1.854	3.748	0.038*
Row	3	4.032	1.466	0.315
Column	3	13.177	36.601	0.000***
Treatment	1	0.044	0.442	0.575
Experiment \times Row	6	5.500	3.707	0.009**
Experiment \times Column	6	0.720	0.485	0.813
Experiment \times Treatment	2	0.198	0.401	0.674
Error	24	5.935		

*** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$.

Column 1	Column 2	Column 3	Column 4
7.42	18.33	20.33	31.92

The significant Column effects in these experiments were similar to those in previous flume experiments with *Capitella* sp. I larvae (Butman and Grassle, 1992; Grassle *et al.*, 1992a) and are believed to be a consequence of interactions between *Capitella* sp. I larval swimming behavior and a weak cross-stream flow near the flume bottom, which tends to concentrate larvae toward the inner flume wall. The significant leading Row effect has been attributed to the tendency for *Capitella* sp. I larvae to settle in the first attractive sediment they contact, as seen in previous flume studies (Butman and Grassle, 1992; Grassle *et al.*, 1992a).

4. Discussion

This study explored how habitat selection in flowing water by settling larvae of *Capitella* sp. I, one of the most widely distributed and opportunistic species in the genus, might help to explain its distribution and population dynamics. Under these experimental conditions, adult *Capitella* sp. I had no direct effect on conspecific larval settlement. The experimental density ($10 \text{ adults} \cdot 11.22 \text{ cm}^{-2} = \sim 9,000 \text{ m}^{-2}$) was within the range of field densities of this species (e.g. $200,000 \text{ m}^{-2}$, Grassle and Grassle (1974); and $5,000 \text{ m}^{-2}$, Fleming (1989); $55,000 \text{ m}^{-2}$, Tsutsumi (1990)), which include subadults. Nonetheless, we cannot rule out the possibility that higher adult densities could have an effect.

These experiments also showed that the presence of adults of a deposit-feeding bivalve, *Tellina agilis*, and a suspension-feeding bivalve, *Mulinia lateralis*, had no effect on *Capitella* sp. I larval settlement at the single experimental density tested. Moreover, the modest sediment reworking by *T. agilis* had no effect on larval settlement. The bivalve density used in the experiments (one adult per 11.22 cm^{-2} , equivalent to 900 individu-

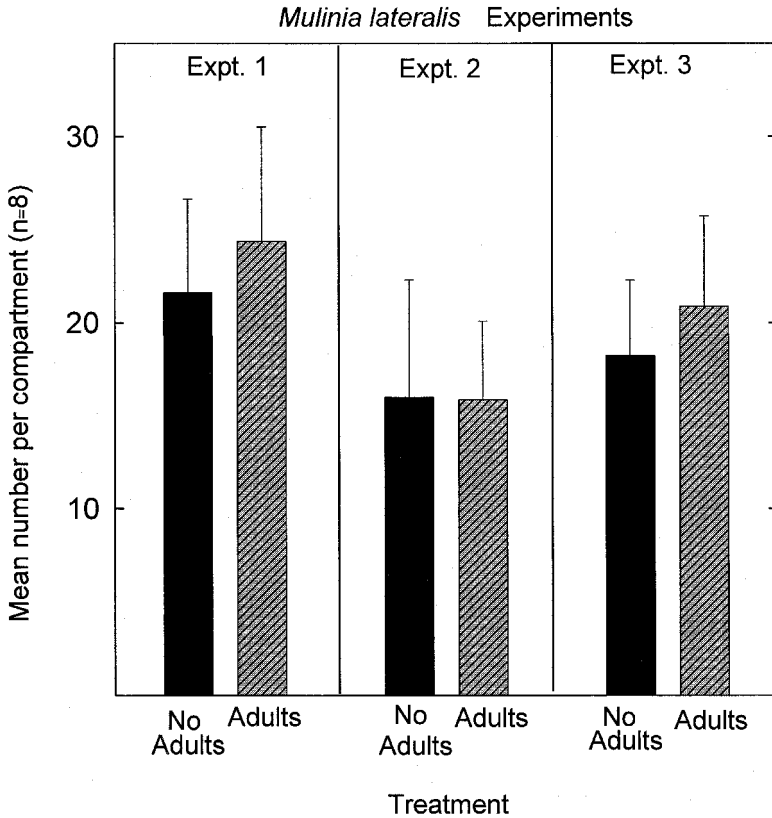


Figure 3. Results from individual experiments with and without *Mulinia lateralis* adults. Bars denote means ($n = 8$) and lines above bars denote 1 standard error. Each panel of plot is a separate experiment.

als m^{-2}) approximates densities measured in the field for both *T. agilis* (e.g., McCall, 1977; Rhoads *et al.*, 1978), and *M. lateralis* (e.g. Reid, 1979). The latter has such large temporal fluctuations in abundance (e.g. Sanders, 1956; Levinton and Bambach, 1970; Luckenbach, 1984), however, that it cannot be characterized by a “typical” density. Given these fluctuations, it would be worthwhile to test for negative effects on *Capitella* sp. I settlement at higher densities.

The neutral effect of *Capitella* sp. I, *Tellina agilis*, and *Mulinia lateralis* adults on *Capitella* sp. I larval settlement certainly does not close the door on *Capitella* sp. I adult-larval interactions. These experiments were a first-step toward evaluating effects on infaunal adults on *Capitella* sp. I larval settlement. It would be reasonable to test higher densities of adult *Capitella* sp. I and *M. lateralis*, as well as sediment that has been more extensively reworked by *T. agilis*. There are also limitations to the experiments conducted here. For example, whereas manipulation probably had little effect on the very robust

Capitella sp. I fecal pellets, the physical and chemical characteristics of the sediments reworked by *T. agilis* may have been altered by this procedure. Finally, high variances and low replication, particularly in the *Tellina* experiments where there were only two replicates, result in low power for detecting significant treatment effects.

A variety of other infaunal species have reciprocal distributions to that of *Capitella* sp. I. We selected infaunal bivalves to contrast with adult *Capitella* sp. I because bivalves tend to rework sediments differently than polychaetes. Large quantities of sediment can be processed by bivalve siphons, material that may be defecated as pellets or loosely bound pseudofeces. The bivalves we chose also include a suspension and a deposit feeder, which may potentially influence larval settlement via different mechanisms (e.g. Woodin, 1976), and provide different sorts of waterborne (e.g. Zimmer-Faust and Tamburri, 1994) or sediment geochemistry (e.g. Woodin *et al.*, 1998) cues.

The only significant effect in this study was that settlement was lower in sediment heavily pelletized by *Capitella* sp. I adults compared to unpelletized sediment. Nevertheless, a substantial number of larvae settled in the pelletized sediments—roughly half of those settling in fresh sediment. These results suggest that whatever labile organic matter is present in organic-rich sediments and vital to *Capitella* sp. I larval settlement and perhaps juvenile growth, not all of it is destroyed by passage through the worms' guts and some is still present in the fecal pellets. A previous experiment showed that diluting by 64% an attractive, organic-rich sediment with a low-organic glass bead mixture did not reduce larval settlement, thus suggesting that a relatively small amount of labile organic matter may be sufficient to induce larval settlement (Grassle *et al.*, 1992a).

Nonetheless, results of two recent studies of *Capitella* sp. I larval settlement in small-volume, still-water experiments (similar in scale to our competency tests) suggest that larvae may settle in sediments with insufficient organic matter for survival and growth under certain conditions (Cohen and Pechenik, 1999; Linton, 1999; Taghon and Linton, 1999). But, whether larval selectivity is tested in flow or still water makes a substantial difference in the capacity of larvae to select among sediment treatments (Grassle and Butman, 1989; Snelgrove *et al.*, 1993; Taghon and Linton, 1999), suggesting caution in interpreting still-water data. Moreover, we have shown that the results obtained in flume-flow experiments with *Capitella* spp. I and II (Grassle and Butman, 1989), are also applicable to the field (Snelgrove *et al.*, 1999). These results echo the findings of Vetter (1996). His enrichment experiments on a sandy bottom showed that members of the ambient community were unresponsive to sediment patches enriched with several different sources of organic matter and generally declined in abundance, while *Capitella* spp. from sources outside the community showed marked increases in abundance.

Gut passage of the labile organic matter that probably contains the cue for *Capitella* sp. I larval settlement, and that is essential for worm growth and reproduction, apparently results in pelletized sediment that reduces larval settlement. Alteration of sediment via gut passage may thus contribute to sharp declines in *Capitella* spp. populations observed in both laboratory and field studies.

Phillips and Tenore (1984) found that larval settlement in still water on isolated fecal pellets was similar to settlement on aggregates of disrupted fecal pellets, and was not different from controls without added organic matter. Maximal settlement was found in treatments with the processed cereal used as a source of organic matter for adult worms. This pattern suggests that the fecal pellets contained less of the settlement cue found in the cereal.

Sediment quality, rather than the presence of the adults themselves, apparently depresses *Capitella* sp. I larval settlement. Heavy sediment reworking modifies bottom sediments in a number of ways. Water and oxygen content are increased, organic content is decreased and modified, effective grain size is increased, and bacterial populations increase (e.g. Rhoads, 1974). In our study, grain size, per se, was unlikely to be a key factor given that previous flume studies have shown that *Capitella* sp. I larvae choose an organic-rich treatment over an organic-poor treatment with similar grain size distributions (Butman *et al.*, 1988a; Butman and Grassle, 1992; Grassle *et al.*, 1992a). Previous studies also showed that water content of sediment had no effect on settlement (Grassle *et al.*, 1992a). Thus, the nature of the organic matter in sediments is the key factor with respect to *Capitella* sp. I settlement and growth (Grémare, 1994). Unfortunately, organic matter is one of the more difficult aspects of sediments to characterize (Mayer *et al.*, 1995). In deep-sea experiments, Snelgrove *et al.* (1992) showed that settlement of *Capitella* spp. in sediments enriched with *Thalassiosira* sp. was significantly greater than in sediments enriched with *Sargassum* sp. or in azoic ambient sediments. This result is similar to those of Tenore and co-workers showing that the source of organic detritus has a significant effect on *Capitella* sp. I growth and reproduction, and argues for the importance of small, labile, high nitrogen particles (Tenore *et al.*, 1984; Marsh *et al.*, 1989).

The results of these experiments suggest that the boom and bust cycle of *Capitella* sp. I settlement, growth, and reproduction is less likely to be related to the presence of adults of conspecifics or of other species (at least for the densities tested here) per se, but may be largely an intrinsic function of the availability of labile organic matter in sediments. In some physically disturbed sediments, and in sediments largely defaunated by pollution or hypoxic or anoxic conditions, certain compounds associated with labile organics may enhance larval settlement, juvenile growth, and individual fecundity at first reproduction. To the extent that this organic matter becomes reduced or unavailable through a diminution in input, competition from sedimentary bacteria (Plante *et al.*, 1990), or pelletization into low-organic, long-lived fecal pellets, larval settlement may be reduced, individual growth slowed, and fecundity reduced. It is unknown, however, whether or not any of the molecules that provide the cue for larval settlement are the same as the micronutrients whose concentrations correlate well with growth. Because experimental evidence indicates that *Capitella* sp. I larvae preferentially settle in sediments characteristic of habitats where adults occur in high abundances, but at a reduced level in heavily reworked sediments, one or more of the compounds that differ between fresh and reworked sediment is likely the settlement cue. It is also possible that the pelletized sediment contains a settlement

suppressant. In either case, the stage is set for future studies of sediment chemistry to identify cues for settlement of perhaps the most opportunistic and cosmopolitan benthic marine organism.

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