



Relationship between sediment organic content, metamorphosis, and postlarval performance in the deposit-feeding polychaete *Capitella* sp. I

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Abstract

Chemical cues induce metamorphosis for the larvae of many benthic marine invertebrate species. These cues help to place organisms into habitats that will allow for rapid growth and increased reproductive success. This study was designed to examine the correspondence between induction of metamorphosis and post-metamorphic success in the deposit feeding polychaete *Capitella* sp. I. Larvae were offered substrates with organic content reduced by 50, 75, 90 or 95% to examine inductive ability. Post-metamorphic success was assessed as juvenile growth rate, time to first brood production, and fecundity. Larvae did not consistently choose the substrate with the highest organic content, and often metamorphosed sooner in response to substrates with insufficient organic material for optimal growth and reproductive success. These findings suggest that, while the cue for metamorphosis is probably organic and bound to fine particulates, the larvae of *Capitella* sp. I cannot assess the concentration of organic material necessary to support subsequent growth and development. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: *Capitella*; Larvae; Metamorphosis; Polychaete; Substrate selection

1. Introduction

The larvae of many benthic marine invertebrate species metamorphose in response to specific chemical cues that are associated with the appropriate habitat for juveniles or adults (reviewed by Pawlik, 1992). While the ability of larvae to discriminate among

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substrates is generally assumed to be adaptive (e.g., Thorson, 1950; Scheltema, 1961; Meadows and Campbell, 1972; Crisp, 1974), few studies have documented the fitness consequences of metamorphosing in response to cues presumed to be of lower quality. In one of the first and most detailed studies, Olson (1983) found that lighting conditions influenced metamorphosis by larvae of the colonial ascidian *Didemnum molle*, and that the choices made by larvae dramatically influenced postmetamorphic survival. More recently, Stoner et al. (1996) examined the relationship between substrate selectivity and juvenile growth rates in the queen conch, *Strombus gigas*. Larvae of the marine polychaete *Capitella* sp. I also lend themselves well to such studies.

Capitella sp. I is an opportunistic deposit feeder, often found at high concentrations in disturbed, soft sediment environments (Grassle and Grassle, 1976; Levin et al., 1996). The lecithotrophic larvae are competent to metamorphose within 15–30 min of being released from the parental brood tube (Butman et al., 1988; Dubilier, 1988; Pechenik and Cerulli, 1991) but postpone metamorphosis for at least several days in clean dishes in the absence of sediment (Butman et al., 1988; Pechenik and Cerulli, 1991). Juvenile growth rates and adult fecundity vary with food quality for this species (Grémare et al., 1988; Marsh et al., 1989; Grémare et al., 1989; Qian and Chia, 1991; Bridges, 1996); therefore we predicted that the larvae of *Capitella* sp. I would preferentially metamorphose into sediments of high organic content, and particularly into those substrates supporting the most rapid growth and highest fecundities. Conversely the larvae should not be triggered to metamorphose into sediments whose organic content is too low to support growth and the attainment of reproductive maturity. Although larvae of this species are thought to metamorphose in response to organic components of the sediment (Dubilier, 1988), the nature of the metamorphic cue has not been fully defined, and the relationship between sediment of reduced organic content, larval metamorphosis, and postmetamorphic performance has not been determined.

The goals of this study were: (1) to determine whether the metamorphic cue for *Capitella* sp. I is water soluble or bound to particulates in mud, (2) to determine whether the larvae metamorphose selectively into sediments of particular organic contents, and (3) to determine the relationship between substrate selectivity and postmetamorphic survival, growth, and fecundity.

2. Materials and methods

2.1. Experimental conditions

The experiments were mostly performed between September 1995 and April 1996. Throughout this study, seawater was filtered to 0.45 μm before use. All mud used to feed adults and trigger metamorphosis was collected in September, 1995, from Little Sippewissett Marsh, Cape Cod, MA, where members of this species occur naturally. The mud was forced through a 1-mm mesh sieve to remove debris, and frozen for at least several days to kill all animal residents. Aliquots of the frozen mud were thawed to room temperature and then aerated by vigorous mixing before use (Butman et al., 1988; Dubilier, 1988; Levin et al., 1996).

Ten experiments were conducted. All experiments were performed at room temperature (22°C). For each experiment, larvae were obtained from a single brood and were usually used within 24 h of release from the brood tube. Larvae were distributed among 2 1/2 in. diameter glass dishes (Carolina Biological Supply Co.) half filled with 0.45- μ m filtered seawater (~30‰ salinity).

2.2. Obtaining larvae

Laboratory-reared adults of *Capitella* sp. I were obtained from Dr. J.P. Grassle, Rutgers University, and maintained in several glass dishes at 20°C, with a photoperiod of 12:12-h light/dark. Once each week, the seawater in each dish was replaced with freshly aerated seawater and adults were fed with several grams of mud. Adults were examined for production of brood tubes at least once each week; brooding females were isolated and monitored daily until larvae were released.

2.3. Defining settlement and metamorphosis

The larvae of *Capitella* have highly visible prototrochal and telotrochal ciliary bands. In all experiments, ‘metamorphosis’ was defined as the loss of both ciliary bands. ‘Settlement’ refers to cessation of swimming, whether or not larvae have metamorphosed.

2.4. Characterizing the cue for metamorphosis

2.4.1. Experiment 1. The effects of ashed mud and mud-conditioned seawater on settlement and metamorphosis

Larval response was examined in response to the following treatments: 1 g of unadulterated mud (‘100% mud’) per dish, 1 g of ashed mud (combusted for 6 h at 500°C to remove all organic matter), mud-conditioned seawater (seawater exposed to mud overnight and then passed through a 1.2- μ m filter), and a seawater control (seawater filtered to 0.45 μ m). Three replicates of ten larvae per dish were used for each treatment. The larvae were examined for settlement and metamorphosis every 15 min for 1 h.

2.4.2. Experiments 2, 3 and 4. Water solubility of the cue for settlement and metamorphosis

Experiment 2. Four replicates of ten larvae per dish were assigned to one of four treatments: two adult worms in filtered seawater, 1 g of unadulterated mud, mud-conditioned seawater, and a filtered seawater control. The larvae were observed for settlement and metamorphosis at 15-min intervals for 1 h and then again at 3 h.

Experiment 3. For the third experiment, experiment 2 was repeated using larvae 2 days post-release; larvae were examined for settlement and metamorphosis every 30 min for 2 h.

Experiment 4. Three replicates of ten larvae per dish were exposed to mud-conditioned seawater that had been passed through filters of three different pore sizes (1.2,

0.45, 0.22 μm) and a seawater control. Larvae were examined for settlement and metamorphosis each hour for 4 h.

2.5. Effect of substrate organic content on metamorphic selectivity

Experiments 5–10. To establish whether larvae of *Capitella* sp. I can distinguish among substrates differing dramatically in organic content, we tested responses to the following substrates: unadulterated mud ('100% mud'); ashed mud (combusted at 500°C for 6 h, termed '0% organic'); substrates with 5, 10, 25, and 50% organic content obtained by mixing ashed mud with different amounts of unadulterated mud; and a filtered seawater control. Mud dry weight was equivalent to 1/3 of the wet weight, so to make a 50% organic mixture, 0.33 g of ashed mud was added to 1 g of wet, unadulterated mud. At least three replicates of ten larvae per dish were used for each treatment. The larvae were observed for settlement and metamorphosis every 15 min for 1 h. In experiments 6, 8, and 10, larvae were also examined after 2–24 h of exposure to the experimental treatments.

These experiments were considered tests of larval substrate selection. Each larva in each treatment had the option to settle and metamorphose on the available substrate, or to delay metamorphosis. In addition, because the larvae for each experiment were genetically similar (siblings) and randomly distributed among treatments, we assumed that the larval behavior in each treatment was representative of the behavior of all the larvae in the brood.

2.5.1. Effect of substrate organic content on juvenile performance

Juvenile performance was assessed by monitoring juvenile growth, juvenile survivorship, time to first brood production, and fecundity over 54 days for the individuals in three of the above experiments (experiments 5, 7, and 9). Freshly filtered seawater and oxygenated mud were provided weekly. Mud was provided in excess, so that juveniles were never starved between food and water changes.

Juvenile growth rates were estimated nondestructively once a week for 54 days by counting the number of segments and measuring the width at the widest point for each individual (Qian and Chia, 1992; Bridges, 1996). Individual biomass was determined at the end of the experiment as another index of growth. To determine biomass, the worms were first rinsed quickly with deionized water to remove any adhering salt or mud and then placed individually in preweighed aluminum foil pans. Samples were then dried at 55°C overnight and subsequently weighed to the nearest 10 μg on a Cahn 21 electrobalance. The animals were then returned to the oven for several hours and some were selected at random for reweighing, to check that no further weight loss occurred (it did not). Finally, the worms were ashed (at 500°C for 6 h) and reweighed in order to calculate ash-free dry weight. Thus the weights used for analysis did not include substantial amounts of inorganic material, such as the ash from mud that might have been in the animal's gut. The relationships between segment width, segment number, and individual organic content were evaluated to determine the best nondestructive estimate of worm organic content. Fecundity was determined by counting the number of

larvae released from the first brood produced by at least 50% of the females in each treatment.

2.5.2. Data analysis

Data were analyzed using either unpaired *t*-tests, or ANOVA and Tukey–Kramer multiple comparisons tests, where appropriate, using InStat 4.0 for DOS and Prism 2.0 for Windows (GraphPad Software, Inc.). Kruskal–Wallis nonparametric analyses were performed as necessary using StatView 4.5 for Macintosh (Abacus Concepts).

3. Results

3.1. Is the metamorphic cue water soluble?

Whereas all larvae metamorphosed in response to 100% mud within 3 h of exposure in all experiments, the larval responses to mud-conditioned seawater differed between experiments. In experiment 1, comparable numbers of larvae metamorphosed in response to 100% mud and to mud-conditioned seawater by the end of 1 h (Fig. 1). In experiment 2, however, significantly more ($p < 0.05$) larvae metamorphosed in the presence of 100% mud than in the presence of mud-conditioned seawater even by the end of 3 h (Fig. 2A). In both experiments, most individuals remained as swimming

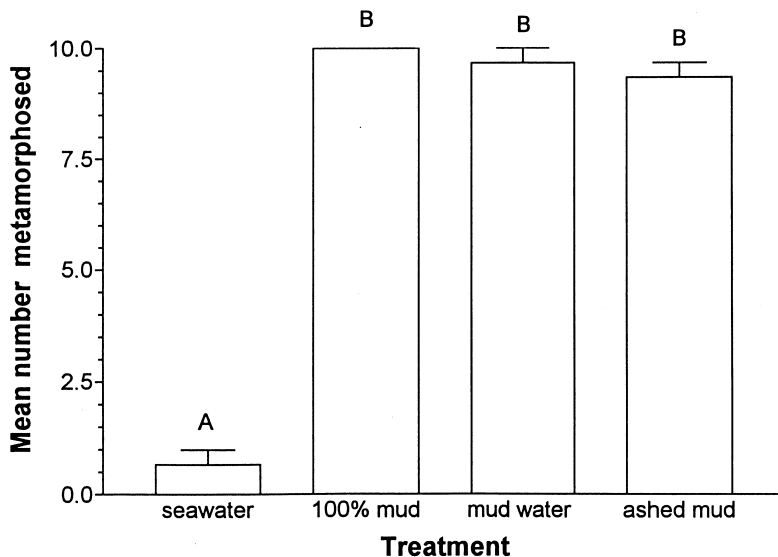


Fig. 1. The average number of *Capitella* sp. I larvae that metamorphosed within 1 h at 22°C in the presence of unadulterated mud, ashed mud, mud-conditioned seawater (1.2- μ m filtered), and a seawater control. Each bar represents the mean of three replicates with ten larvae per replicate. Error bars represent one standard error above the mean. Different letters represent significant differences among means ($p < 0.001$, Tukey–Kramer multiple comparisons test following one-way analysis of variance).

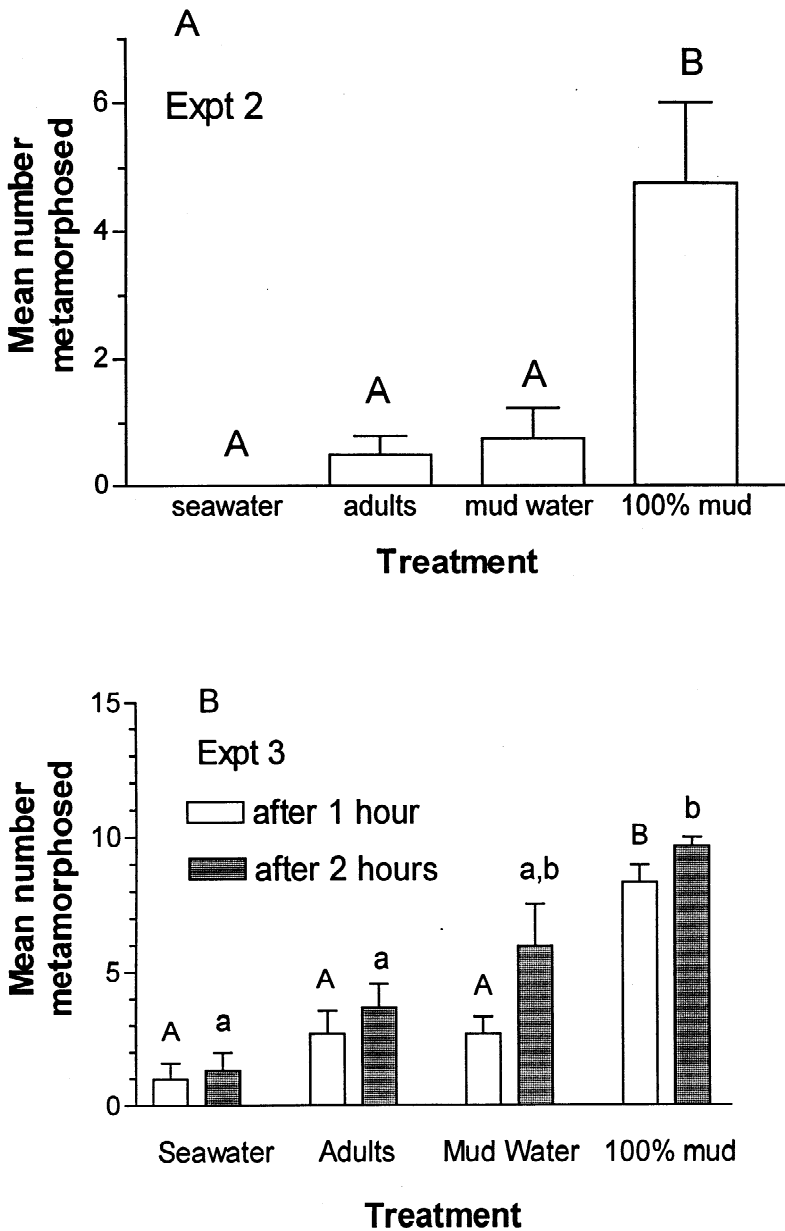


Fig. 2. The average number of *Capitella* sp.I larvae that metamorphosed when exposed to adults, 100% mud, mud-conditioned seawater (1.2- μ m filtered), and a seawater control at 22°C. Each bar represents the mean of three (A) or four (B) replicates with ten larvae per replicate. Error bars represent one standard error above the mean. (A) Metamorphosis after 3 h. Different letters above bars represent means that differ significantly ($p < 0.05$) from each other (Tukey–Kramer multiple comparisons test following one-way analysis of variance; $F = 10.22$; d.f. = 3,12; $p = 0.0013$). (B) Metamorphosis after 1 and 2 h. Different letters represent significant difference among means ($p < 0.05$, Tukey–Kramer multiple comparisons test).

larvae in the seawater control treatment. In contrast, larvae were more responsive to 100% mud during the first hour in experiment 3; the significant difference in larval response to 100% mud and to mud-conditioned seawater vanished by the end of the second hour (Fig. 2B). Larvae demonstrated no significant metamorphosis in response to adults (Fig. 2).

Filtering mud-conditioned seawater through three different pore sizes (1.2, 0.45, and 0.22 μm) resulted in a significant difference in the number of larvae that metamorphosed across treatments (Fig. 3; Kruskal–Wallace, $df = 3$, H (tied) = 10.72, p (tied) = 0.018). None of the larvae in the seawater control or the 0.22- μm filtered mud-water metamorphosed during the 4 h experiment (Fig. 3).

3.2. Sensitivity to substrates of different organic contents

Significantly more larvae metamorphosed in response to muds of 50, 25 and 10% organic content than to 100% mud by the end of 1-h exposures in experiments 5–8 ($p < 0.02$) (Figs. 4 and 5). By the end of 2 h, however, the differences in response were generally no longer significant (e.g. Fig. 4B; Tukey–Kramer, $q = 0.9129$, $p > 0.05$). In both experiments 7 and 8, substantial numbers of larvae metamorphosed in mud of only 10% organic content within 2 h (Fig. 5), but when the organic content of the mud was

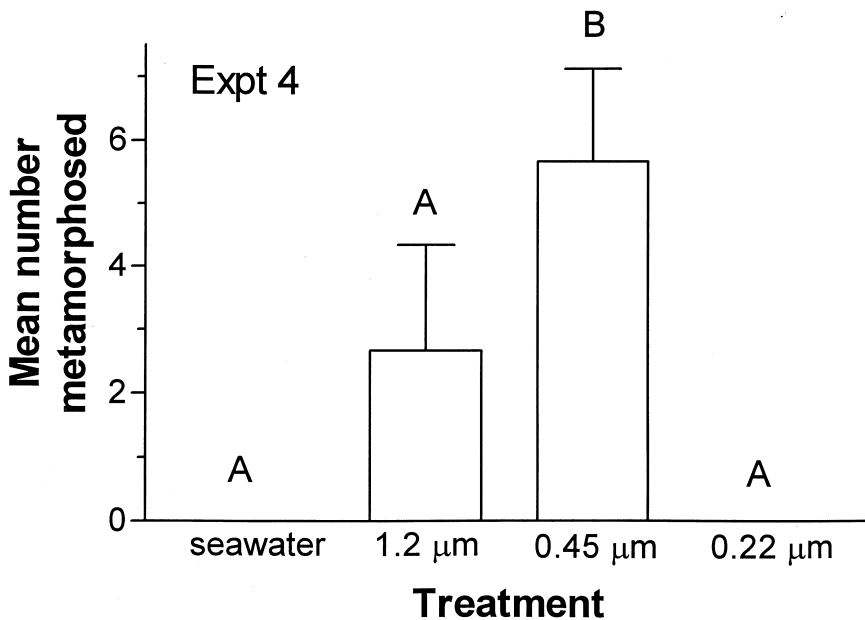


Fig. 3. The average number of *Capitella* sp. I larvae metamorphosed after 4 h in 1.2-, 0.45-, and 0.22- μm filtered mud-conditioned seawater and a seawater control at 22°C. Each bar represents the mean of three replicates with ten larvae per replicate and the error bars show one standard error above the mean. Different letters represent significant differences among means (Tukey–Kramer multiple comparisons test).

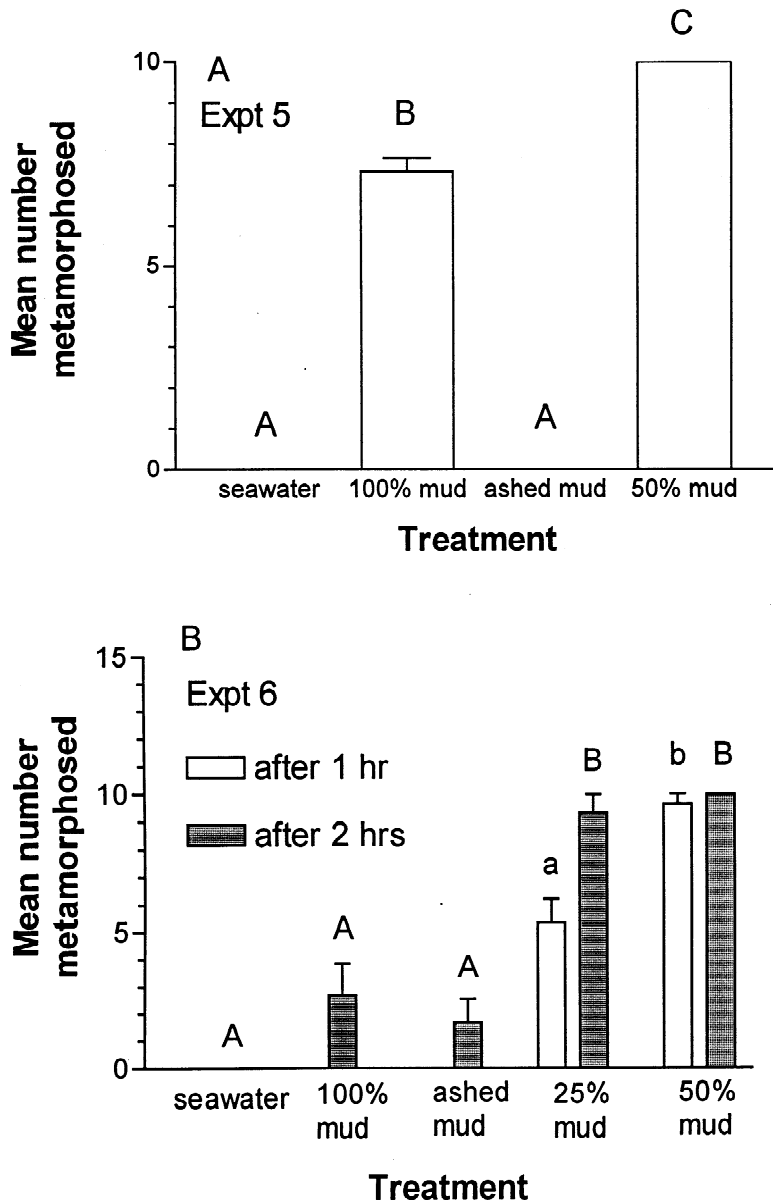


Fig. 4. The average number of *Capitella* sp. I larvae that metamorphosed at 22°C (A) within 1 h of exposure to seawater, ashed mud, 100% organic mud or 50% organic mud; (B) metamorphosed after 1 and 2 h of exposure to 25 and 50% organic mud treatments. Each bar represents the mean of three replicates of ten larvae per replicate, and the error bars show one standard error above the mean. Different letters represent significant differences among means (Tukey–Kramer multiple comparisons test).

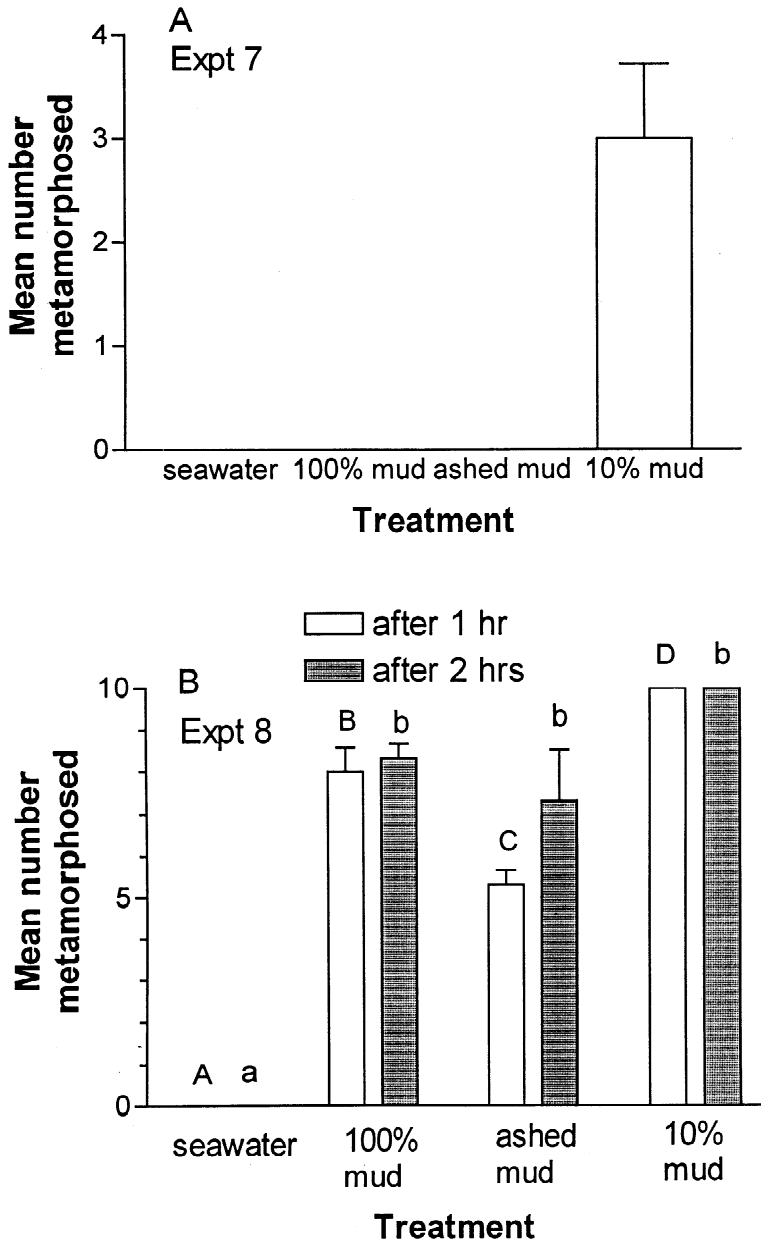


Fig. 5. The average number of *Capitella* sp. I larvae that metamorphosed when exposed to ashed mud, 100% organic mud, 10% organic mud or a seawater control at 22°C (A) after 1 h where each bar represents the mean of four replicates of ten larvae per replicate and one standard error above the mean, and (B) after 1 and 2 h where each bar represents the mean of three replicates of ten larvae per replicate and one standard error above the mean. Different letters represent significant differences among means (Tukey–Kramer multiple comparisons test).

decreased to 5%, the substrate was no longer an effective cue for metamorphosis during a 1-h exposure (Fig. 6A).

With the exception of experiments 1 and 8, larvae did not metamorphose in appreciable numbers in response to ashed mud in the first 1–2 h of exposure. In a follow-up experiment conducted April 1998 (experiment 10), larvae remained reluctant to metamorphose in response to ashed mud for at least 24 h (Fig. 6B). However, all individuals metamorphosed in response to ashed mud within 24 h in all earlier experiments.

3.3. Juvenile growth rates on substrates of different organic contents

3.3.1. Biomass as an index of growth

No individuals survived more than 7 days following their metamorphosis in ashed mud or in the seawater controls. Juveniles grew as rapidly on mud of 50% organic content as on 100% mud (two-tailed unpaired *t*-test, $t = 0.1923$, $df = 11$, $p = 0.8510$) (Fig. 7). Juveniles grew significantly more slowly, however, on substrates with only 5% organic content (two-tailed unpaired *t*-test, $t = 4.524$, $df = 9$, $p = 0.0014$) or 10% organic content (two-tailed unpaired *t*-test, $t = 10.74$, $df = 21$, $p < 0.0001$) (Fig. 7).

3.3.2. Growth rate as assessed by worm length and width

The number of segments alone was a particularly poor indicator of individual biomass. The best non-destructive method of estimating growth for individuals throughout the experiment required measurement of both segment width and number of segments (regression analysis, $F = 17.67$, $df = 1, 16$, $p = 0.0007$) (Fig. 8C, $r^2 = 0.525$).

Fig. 9 illustrates the trend in juvenile growth rates for individuals that metamorphosed in muds of 50 and 5% organic content. Juveniles in 50% mud grew at a similar rate compared to siblings cultured in 100% mud (Fig. 9A). Juveniles foraging in mud of 5% organic content grew far more slowly than the individuals in 100% mud, and were far smaller at the end of the 62 day experiment (Fig. 9B); similarly slow growth rates were recorded for juveniles reared on mud of 10% organic content (data not shown).

3.4. Influence of sediment organic content on fecundity and time to reproductive maturity

The number of larvae per brood from adults raised on mud of 50% organic content ($\bar{x} = 198.3$ larvae per brood, S.E.M. = 66.56, $n = 4$) did not differ significantly from the number produced by sibling adults raised on 100% mud ($\bar{x} = 292.0$ larvae per brood, S.E.M. = 75.27, $n = 3$) (two-tailed unpaired *t*-test, $t = 0.9297$, $df = 5$, $p = 0.3952$). None of the individuals raised on 5 or 10% mud produced any broods over the 54 days of this experiment.

4. Discussion

Previous experiments indicated that the larvae of *Capitella* sp. I respond very quickly

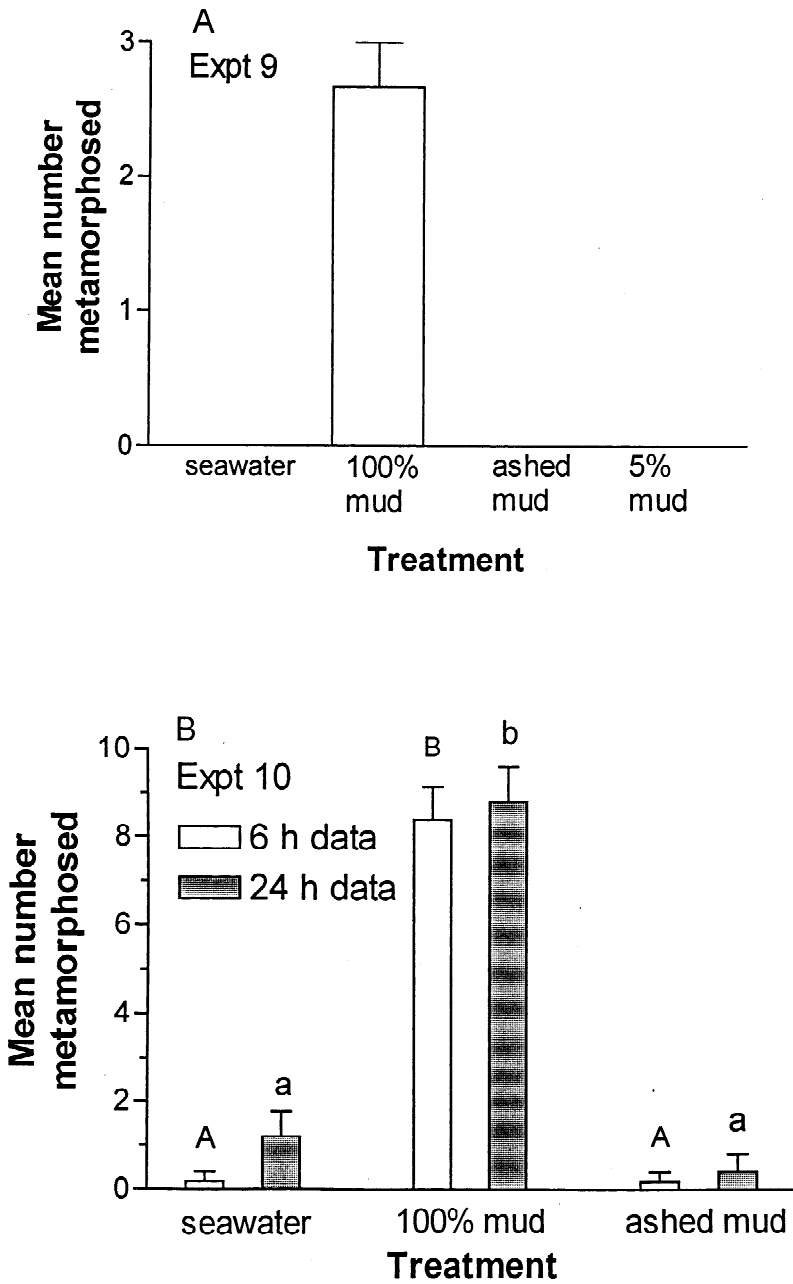


Fig. 6. The average number of *Capitella* sp. I larvae that metamorphosed at 22°C (A) after 1 h in response to ashed mud, full-strength mud, 5% mud and a seawater control, or (B) after 6 and 24 h in response to full-strength, ashed mud, or a seawater control. Bars represent the mean of three replicates of ten larvae per replicate and one standard error above the mean.

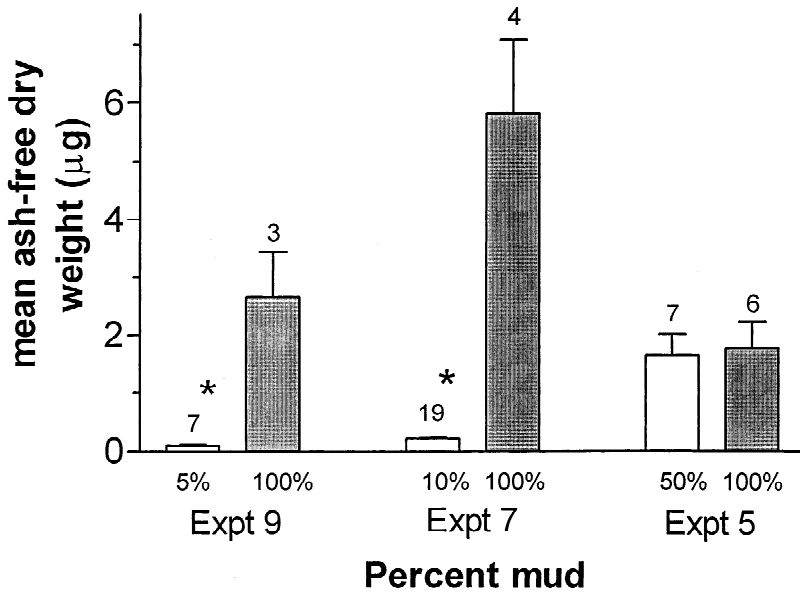


Fig. 7. The ash-free dry weights for *Capitella* sp. I from three different broods raised on substrates with 5, 10, or 50% organic content compared to those of siblings raised on 100% organic mud. Bars represent the mean ash-free dry weight of all individuals in the treatment at the end of the 54-day experiment. Sample size and the standard error of the mean are indicated above each bar. Asterisks represent significant differences between means ($p < 0.01$, t -test).

to sediment with high organic content (Dubilier, 1988; Pawlik, 1992), typically metamorphosing within only 20 minutes at 20°C (Dubilier, 1988). The results of several other studies also showed larval settlement and metamorphosis within minutes of exposure to natural muds (Butman et al., 1988; Grassle and Butman, 1989; Pechenik and Cerulli, 1991). In the present study, the time larvae took to settle and metamorphose in response to 100% mud varied substantially among broods, ranging from 15 min to several hours. Even so, all larvae did metamorphose in response to the mud within 3 h of exposure.

Larvae exposed to water that had been in contact with the organic-rich mud metamorphosed (Figs. 1 and 2B), suggesting that the metamorphic cue might be water soluble. However, a particulate component of the mud is most likely responsible for metamorphic induction since the cue was successfully removed by passage through a 0.22- μ m filter (Fig. 3). Adult *Capitella* sp. I are often found in high concentrations, suggesting a possible gregarious response. In our experiments, there was no evidence for this; neither the presence of adults (Fig. 2A,B) nor juveniles (data from pilot experiments) elicited a significant metamorphic response.

Because larvae in the genus *Capitella* are commonly found in disturbed sediments such as those near sewer outfalls, they are often used as marine pollution indicators (Grassle and Grassle, 1976; Levin et al., 1996). These sediments often have increased organic content, which has been shown to enhance growth and reproductive success in

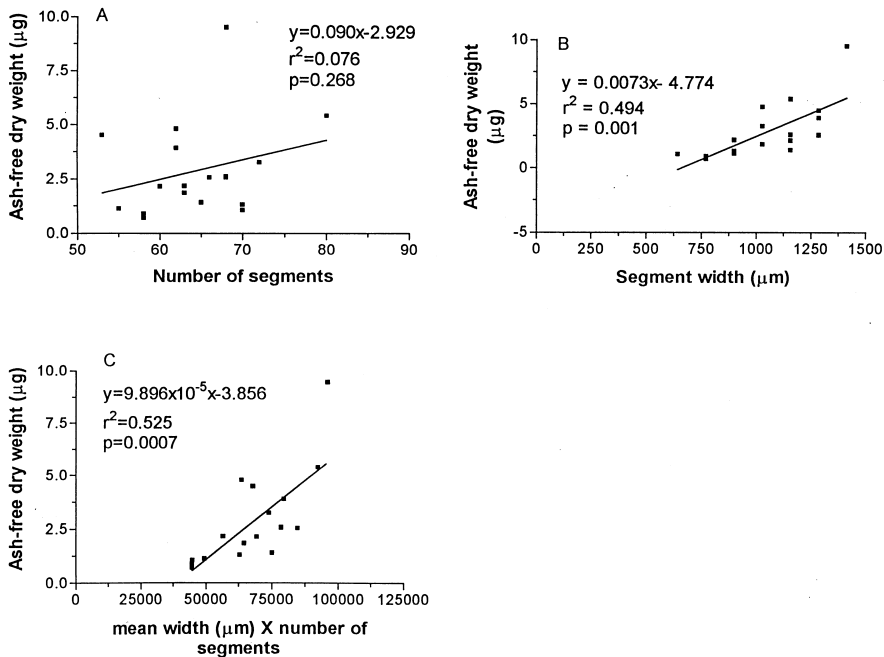


Fig. 8. The relationship between (A) ash-free dry weight and number of segments, (B) ash-free dry weight and width, and (C) ash-free dry weight and width times the number of segments for *Capitella* sp. I raised on 100% organic mud.

Capitella (Grémare et al. 1988; Grémare et al. 1989; Marsh et al. 1989; Bridges et al., 1994; Bridges, 1996), though it is uncertain whether sediment organic content is solely responsible for these effects. For example, Tsutsumi et al. (1990) found that growth of *Capitella* sp. juveniles was independent of absolute organic content but increased with the addition of algal powder to the sediment. Marsh et al. (1989) considered the possibility that increased juvenile growth in *Capitella* sp. I occurs when high organic content of the sediment is combined with micronutrients, because detritus from spring promoted more growth than that from summer. In any case, the cue for metamorphosis is most likely associated with organic sediment. Therefore, the reliance of larvae on an organic, sediment-associated cue coupled with increased juvenile fitness on substrates of high organic content should decrease the likelihood that larvae would metamorphose in response to substrates of low organic content.

Our results disagreed with the prediction of decreased larval metamorphosis in response to substrates with reduced organic content: under the conditions of our experiments, the larvae of *Capitella* sp. I did not always make the 'right' choice (Fig. 1). Surprisingly, larvae often took longest to metamorphose in sediments of the highest organic content (100% mud) (e.g. Fig. 5), even though these sediments supported excellent survival and growth of juveniles. The larvae may have been inhibited from metamorphosing by the high sulfide concentration of 100% mud (Dubilier, 1988), but

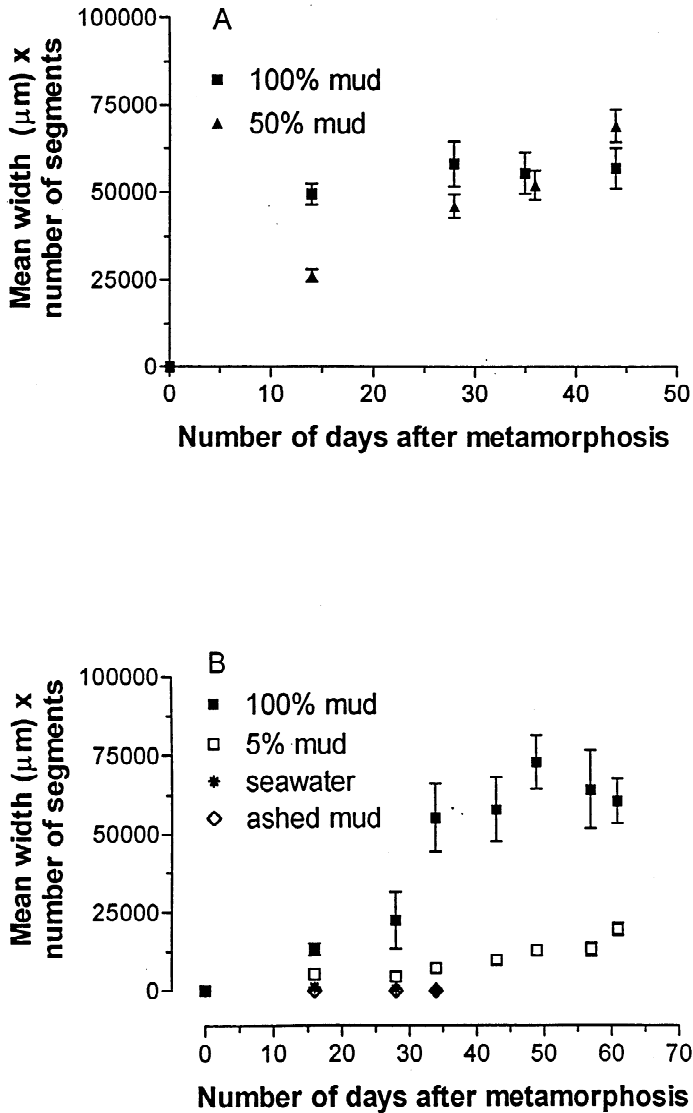


Fig. 9. The growth rate of *Capitella* sp. I (A) raised on mud of 50% organic content compared to the growth rate of siblings raised on 100% mud, or (B) raised on mud of 5% organic content compared to that of siblings raised on 100% mud. Each point represents the (mean width)(number of segments) of all individuals in the treatment and the standard error above the mean ($N = 4-14$ individuals measured for each treatment on each date).

additional experiments where organic content is altered and sulfide concentrations are measured and manipulated must be performed to confirm this hypothesis.

Although larvae did not metamorphose in the ashed mud within the first 1–2 h of

exposure, all larvae metamorphosed in the presence of ashed mud within 24 h. No larvae metamorphosed in the filtered seawater controls during this time. Since many of the larvae in ashed mud treatments took > 12 h to metamorphose, they may have been responding to microorganisms building up in or on the sediment; microbial films promote settlement of larvae of many polychaete species (Pawlik, 1992). However, in two cases in our experiments, larvae exposed to ashed mud metamorphosed as fast as larvae exposed to 100% mud, within 1–2 h of exposure (Figs. 1 and 5B). It seems likely that larvae presented with ashed mud were responding to substrate texture. Grain size is an important metamorphic cue for larvae of the polychaete *Ophelia bicornis* (Gray, 1974).

Juvenile growth rates on the altered substrates did not parallel the larval substrate preferences. Except for the juveniles in mud of 50% organic content, the individuals that metamorphosed in all of the other muds of decreased organic content grew significantly more slowly than those in 100% mud, and they produced no brood tubes during 54 days of monitoring. Juveniles in mud of 50% organic content grew more slowly than the control juveniles for the first month, but they attained similar sizes after about 35 days (Fig. 9A) and produced numbers of offspring statistically comparable to those produced by worms raised on 100% mud. Juveniles maintained on mud of 50% organic content may have compensated for lower organic content of the diet by increasing their ingestion rates. According to optimal foraging theory, ingestion rates increase as protein concentrations increase, thereby allowing deposit-feeding invertebrates to maximize net energy gain per unit time. Results from a feeding experiment by Taghon and Jumars (1984) supported the optimal foraging theory – three species of deposit-feeding polychaetes increased their feeding rates in response to sediments differing only in protein content. Forbes et al. (1994) also found a positive relationship between feeding rates for *Capitella* sp. I individuals and the protein content of the substrate under well-oxygenated conditions. However, when the amount of oxygen available in the sediment was low, ingestion rates increased in the presence of low food concentration. To determine whether *Capitella* sp. I can compensate for decreased concentrations of organics by increasing ingestion rates, studies of the relationship between organic content of the sediment, juvenile egestion rate, and juvenile growth rate must be performed.

Given that muds lower than 50% in organic content resulted in dramatically lower juvenile growth rates and increased time to reproductive maturity, the results from our metamorphic induction experiments were unexpected: the larvae metamorphosed less readily in the presence of 100% mud than in the presence of most substrates with reduced organic content. In several experiments, larvae metamorphosed readily in ashed muds of 0% organic content – substrates in which no worms survived more than a week and in which none reached reproductive maturity.

There have been few studies showing that larval substrate selectivity results in increased survivorship, growth, or fecundity. Olson (1983) showed a clear survival advantage for the substrate selectivity demonstrated by larvae of the colonial ascidian *Didemnum molle*, but Babcock and Mundy (1996) found no correlation between habitat choice and post-settlement survivorship for two species of hermatypic corals, suggesting that there may not be one optimal habitat for juveniles of those species. In another study,

Strombus gigas larvae metamorphosed readily on some substrates that did not support high juvenile growth rates (Stoner et al., 1996). The extent to which substrate selectivity improves fitness in field populations generally remains to be examined.

Throughout our experiments, as many as 75% of the larvae from a given brood of *Capitella* sp. I were observed to settle and metamorphose within 24 h on glass dish surfaces in filtered seawater. This was surprising since *Capitella* larvae have been routinely observed to delay metamorphosis for several days in the absence of a mud cue (Butman et al., 1988; Pechenik and Cerulli, 1991). The larvae may have been responding to some physical cue, such as light or temperature, but this is unlikely given that all experiments were performed under similar conditions to those described in previous studies (see Pechenik and Cerulli, 1991). Possibly, some individuals may not require a cue for settlement and metamorphosis, and are therefore physiologically different from those larvae that do need a chemical cue. Alternatively, individuals that produce larvae that metamorphose without a cue may be an unrecognized subspecies of the genus *Capitella*. The polychaete *Hydroides dianthus* apparently produces some larvae that require a specific cue for metamorphosis and some that do not (Toonen and Pawlik, 1994), although it is not clear whether or not both types of larvae are produced by individual females.

The propensity of some larvae of *Capitella* sp. I to metamorphose in the absence of a mud cue may have a genetic basis, but if it does, preliminary experiments have shown that the pattern of inheritance is not simple (R. Cohen, unpublished data). When individuals that metamorphosed in the absence of mud reached adulthood and reproduced, their broods contained both types of larvae, some that did and many that did not metamorphose without sediment. Further testing is necessary to determine whether there is a genetic basis for larval metamorphosis in the absence of mud, as well as isozyme analyses to establish whether these 'deviant' individuals belong to *Capitella* sp. I or to another sibling species.

This study reveals that larvae of *Capitella* sp. I do not preferentially settle and metamorphose in response to substrates that always confer the highest growth rates and highest fecundities, although they did postpone metamorphosis in sediments of the very lowest organic content tested (5% organic content and 0% organic content). These data counter the general expectation that substrate selectivity improves post-metamorphic fitness. It is possible that larvae of *Capitella* sp. I do not often experience substantial substrate selection pressure in the field, as they are competent to metamorphose within minutes of their release into the plankton (Dubilier, 1988; Pechenik and Cerulli, 1991), and are therefore likely to recruit into the parental population. Just how often and how far the larvae of this species disperse from the parental habitat in the field remains to be determined. Population data from a study by Tsutsumi (1990) imply that despite the ability for widespread dispersal by *Capitella* sp. larvae, the population they studied in an organically enriched mudflat was maintained without recolonization from other habitats over 1 year. Thus, the large concentrations of *Capitella* sp. I in sediments of high organic content probably owe more to rapid growth and early maturation in such habitats than to substrate preferences exhibited by larvae derived from distant sites (Levin et al., 1996).

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