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Enhanced larval settlement of the hard clam *Mercenaria mercenaria* by the gem clam *Gemma gemma*

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ABSTRACT: The presence of dense assemblages of *Gemma gemma* enhanced settlement of *Mercenaria mercenaria* larvae in laboratory experiments. There was a tendency toward increased settlement of hard clam larvae with increasing density of gem clams. Microscopic examination showed that increased settlement did not result from trapping or entanglement in sticky secretions from gem clams. Enhanced settlement in the presence of gem clams was persistent in both gently aerated and recirculated waters, and in both sand and muddy sand, suggesting that *M. mercenaria* larvae could recognize settlement cues associated with *G. gemma* in various habitats and hydrodynamic conditions. Preferential settlement in sediment previously exposed to gem clams indicates that gem clams alter sediment in some way to make it attractive for larval settlement. In addition, increased settlement in the presence of empty gem clam shells in sediment suggests that settlement cues are properties of the shell, although the nearly significant settlement with gravel particles suggests that physical cues, such as grain size and bottom roughness, may play a role. Thus, this study demonstrates dense assemblages of small suspension feeders can enhance larval settlement of another bivalve species.

INTRODUCTION

Abundance and distribution of the hard clam *Mercenaria mercenaria* have been extensively studied for the appropriate management of this commercially important species (Carriker 1961, Hibbert 1976, 1977, Walker & Tenore 1984). Most work, however, has been focused on juvenile and adult stages. Due primarily to difficulties in sampling, identification, and experimental manipulation, there have been relatively few studies on settlement and early post-settlement stages (Peterson 1986, Butman et al. 1988, Wilson 1990).

Larval recruitment of *Mercenaria mercenaria* may play an important role in determining spatial patterns and abundance of adult populations. Many researchers have reported sharp declines within a few months after settlement in the density of hard clams (Carriker 1959) and other infaunal species (Thorson 1966, Muus 1973, Shaffer 1978, Möller & Rosenberg 1983, Luckenbach 1984, Jensen & Jensen 1985). These declines have been attributed to various biological and physical factors (reviewed by Thorson 1966).

Established adult infauna may affect recruitment of hard clams and other infaunal species through ingestion or filtration of larvae, sediment reworking, competition and predation. Some studies have demonstrated negative intra- and inter-specific adult-larval interactions on settling or newly settled infaunal species (Williams 1980, Wilson 1980, Brenchley 1981, Levin 1981, Peterson 1982, Gallagher et al. 1983, Luckenbach 1984, Tamaki 1985, Woodin 1985).

Large suspension-feeding bivalves have been implicated in the inhibition of recruitment of planktonic

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larvae of benthic organisms. Woodin (1976) predicted that infaunal species would not attain their highest densities among densely packed suspension-feeding bivalves. Field experiments tested Woodin's prediction, demonstrating negative effects of dense adult population on settlement of their spat, but even in dense assemblages, larvae were not prevented from successful recruitment (Williams 1980, Peterson 1982). In other cases, adults did not affect larval settlement (Maurer 1983, Hunt et al. 1987, Black & Peterson 1988). Dense assemblages of small (few mm) suspension feeders such as *Gemma gemma* have also been implicated in controlling larval recruitment. The gem clam, which grows up to 5 mm in shell length, is one of the most abundant infaunal species in shallow estuarine waters (Bradley & Cooke 1959, Sanders et al. 1962, Sellmer 1967, Green & Hobson 1970, Maurer et al. 1978, Woodin 1981, Thomson 1982, Botton 1984). Adult densities often reach 10^5 ind. m^{-2} in summer months (Bradley & Cooke 1959, Sanders et al. 1962, Sellmer 1967, Green & Hobson 1970, Thomson 1982). It shares with *Mercenaria mercenaria* much of the same habitat and geographic range and the 2 species frequently co-occur, particularly in sandy sediments (Sellmer 1967, Green & Hobson 1970, Greene 1981). It has very short siphons and feeds mostly at the sediment-water interface (Sellmer 1967). Bradley & Cooke (1959) and Sanders et al. (1962) observed the inverse relationship between abundance of *G. gemma* and other suspension-feeding bivalves, and suggested that dense *G. gemma* populations inhibit the recruitment of other suspension-feeding bivalve species by outcompeting the tiny spat for food at the time of settlement. Therefore, *G. gemma* was chosen in this study as a representative infaunal species that may affect the early recruitment of hard clams.

Competitive exclusion of hard clam larvae by densely packed gem clams could conceivably be expected during settlement. Spawning of *Mercenaria mercenaria* occurs during summer months (in mid- and North Atlantic), when *Gemma gemma* density reaches the highest values in temperate waters. The planktonic larval stage lasts 6 d to several wk depending on water temperature. A *M. mercenaria* larva is approximately 200 µm in shell length at the time of settlement (Loosanoff 1959).

In this study, the effect of *Gemma gemma* on larval settlement of *Mercenaria mercenaria* was determined in various experimental conditions which would be experienced by hard clams in the natural environment, and an example of a positive interspecific adult-larval interaction was demonstrated. Furthermore, settlement-inducing factors associated with *G. gemma* were examined.

MATERIALS AND METHODS

Four to five-day-old *Mercenaria mercenaria* larvae were obtained from a hatchery company (Bluepoints Co., Inc.) and cultured in the laboratory until they became competent to settle. *Gemma gemma* (2 to 5 mm in shell length) were collected from the intertidal zone of Flax Pond, a *Spartina* salt marsh on the north shore of Long Island, New York, USA. Both bivalve species were acclimated to experimental conditions for at least 3 d. They were fed *Isochrysis galbana* (clone T-iso, 4 µm) during acclimation and experimental periods. Algal concentration as determined by Coulter Counter (Model TAII) was maintained at 0.5 to 1 × 10^5 cells ml^{-1}.

Medium-sized (250 to 500 µm) sand was used as substratum. This size range of sand was selected because larval or newly settled hard clams (200 to 500 µm) can be easily extracted with repeated vortex mixing and decantation. Sand was dried at room temperature for several weeks and was soaked in filtered seawater for several days prior to use in experiments.

Illumination (12L:12D) was by fluorescent light (Daylight) equipped with a dimming unit to simulate natural crepuscular periods. Dawn and dusk periods lasted 100 min each. Daytime light intensity was approximately 30 µE m^{-2} s^{-1}, which was similar to summer intensity at 1 m depth of Great South Bay, Long Island (Monteleone 1988). Water temperature (20 °C) and salinity (26 ‰) were kept constant throughout the experimental period. Unless otherwise stated, seawater was filtered through a 0.22 µm filter.

Upon completion of an experiment, sediment containing clams was collected by siphoning, preserved with buffered 5 % formalin, and stained with rose bengal. Gem clams were sieved out with a 1 mm sieve and hard clams were extracted by repeated high-speed vortex mixing (5 times, 15 s each time) followed by decantation. No more than 5 cm^3 of sediment was processed each time in a 50 ml plastic centrifuge tube. A capture efficiency experiment determined that >95 % of hard clams were extracted with this method. Clams preserved alive and those preserved dead were counted separately with the aid of a dissecting microscope; only the former were considered for statistical analysis. ANOVA and multiple comparisons among means (Sokal & Rohlf 1981) were used to test for statistical significance of each experimental factor Assumptions for ANOVA were tested and transformations were performed when necessary.

Larval settlement experiments. The purpose of these experiments was to determine whether *Gemma gemma* affects *Mercenaria mercenaria* larval settlement. Experiments were conducted in a 7.8 l Plexiglas aquarium (27.5 × 19 × 15 cm) filled with seawater to a depth of 13 cm. The experimental unit was a small well (3.6 cm in diameter, 1 cm depth) of a 6-well culture dish (12.7 × 8.5 × 1.7 cm) (Falcon).

Effect of *Gemma gemma* on *Mercenaria mercenaria* was studied for a wide range of *G. gemma* densities. Because of seasonal variation in body size, numbers of *G. gemma* for low (27 to 50 clams per 3.6 cm diameter well) and high (110 to 200 clams well^{-1}) densities were determined on the basis of total wet weight (~25 mg cm^{-2} for low and ~100 mg cm^{-2} for high density). Densities of gem clams were within the range occurring in nature (Bradley & Cooke 1959, Sanders et al. 1962, Sellmer 1967, Green & Hobson 1970, Thomson 1982). *M. mercenaria* larvae were added in densities of 3 to 7 larvae ml^{-1}. In addition, effect of dense patches of *G. gemma* was determined in 2 water regimes and in 2 sediment types which would be experienced by hard clams in the natural environment.

Expt 1: effect of Gemma gemma density: The purpose of this experiment was to determine effects of *G. gemma* density in clean sand on *Mercenaria mercenaria* settlement. The aquarium was gently aerated with airstones from 2 opposite sides of the container. Twelve wells in two 6-well plates were filled with prepared sand and used as sediment beds. The entire bottom of each plate, both within and outside the wells, was covered with sand.

Settlement of hard clam larvae was assessed at 0, 50 (250 mg) and 200 (1000 mg) *Gemma gemma* (2.4 mm mean shell length) well^{-1}. Four replicates for each treatment were placed in the wells in a completely randomized design, and the 6-well plates were then placed in the aquarium. One day later, hard clam larvae were introduced. Larvae ranging from 170 to 200 µm in shell length (a few days before the pediveliger stage) were selected because larvae at this size range display active swimming and substrate-selecting behavior. Two to three days later, most larvae had settled and the experiment was terminated. This experiment was conducted 4 times. See Table 1 for size, age, and concentration of larvae and duration of exposure in each trial.

Expt 2: effect of Gemma gemma and water movement: This experiment was conducted to determine whether hard clam larval settlement is affected by different degrees of water movement. In one treatment, seawater was gently aerated with airstones from 2 sides of the container walls as in Expt 1. In the other treatment, seawater was recirculated constantly at 2 l min^{-1} by airlifting (Kinne 1976) through 2 L-shaped PVC tubes at 2 diagonally opposite corners; turnover time was 3.5 min. Settlement was assessed at 0 and 120 (1000 mg) *G. gemma* (2.9 mm mean shell length) well^{-1}. Post-addition sampling showed that 4 larvae ml^{-1} were added to recirculated water, and 3 larvae ml^{-1} added to aerated water. Three replicate wells were run for each of the 4 treatments.

Expt 3: effect in sand and muddy sand: This experiment was conducted to determine the separate and combined effects of *Gemma gemma* and sediment type on *Mercenaria mercenaria* larval settlement. We compared clean sand and muddy sand, 2 sediment types in which both hard clams and gem clams commonly occur. Muddy sand (containing approximately 10 % mud and 1 % organic matter on a dry weight basis) was prepared by mixing clean sand with mud (< 63 µm) collected from the top 1 cm of intertidal mud flat at Flax Pond. Clean sand was prepared as described earlier. For each substrate, settlement was assessed at *G. gemma* densities of 0 and 150 (1000 mg) well^{-1} (2.5 mm mean shell length). There were replicate wells for each treatment in this 2 × 2 experiment, for a total of 12 wells. Treatments were assigned randomly to wells. The overall experimental design was like Expt 1.

Expt 4: response to juvenile Mercenaria mercenaria and adult Gemma gemma: Adult *G. gemma* (~3 mm) were compared to similarly sized *M. mercenaria* for their effect on settlement of hard clam larvae. For each species, settlement was assessed at densities of 0, 27 (250 mg), and 110 (1000 mg) clams well^{-1}. Setup was similar to Expt 1.

Experiments on settlement-inducing mechanisms. Experiments were conducted to elucidate settlement inducing factors associated with *Gemma gemma*. These settlement experiments had similar design to those described above, but differed from them in that *G. gemma* was not present during the *Mercenaria mercenaria* larval settlement period.

Expt 5: response to Gemma gemma-exposed sand: The purpose of this experiment was to determine whether hard clam larvae preferentially settle on sediment previously inhabited by gem clams. Treatments included sand previously exposed to 0, 50 or 200 *G. gemma* (2.4 mm mean shell length) well^{-1}. *G. gemma*-exposed sediment was prepared by keeping gem clams in wells filled with clean sand. Four replicates were prepared for each treatment for a total of 12 wells. After 3 d, during which gem clams were fed, they were picked out of the sediment. The top 5 mm sediment in all wells was stirred with forceps to simulate disturbance caused by picking 200 gem clams. All sediment surfaces were subsequently flattened. *Mercenaria mercenaria* larvae were then introduced and allowed to settle for 3 d.

Expt 6: response to addition of gravel particles: This experiment was done to determine whether hard clam larvae preferentially settle in response to differences in physical properties of sediment, such as particle size and bottom roughness, of the sediment containing gem clams. We chose gravel particles of 2 to 3 mm to mimic

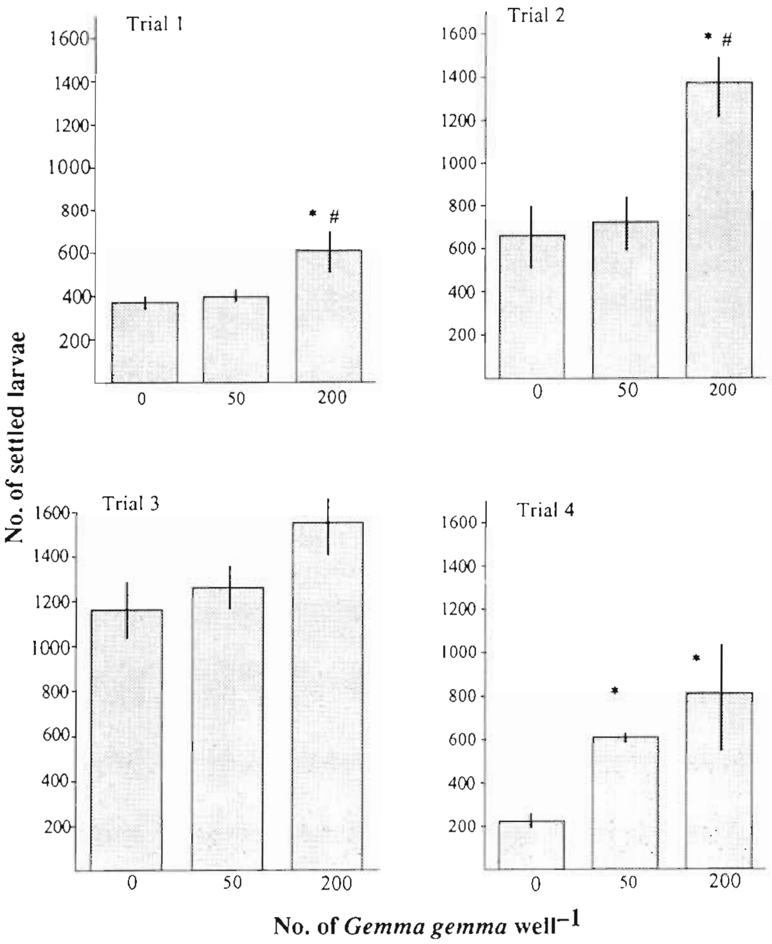

Fig. 1. Expt 1. Effect of *Gemma gemma* on settlement of *Mercenaria mercenaria* larvae. Mean (±1 SE) no. of larvae settled (n = 4) in 4 consecutive trials. Larval concentration in 7 l was 4 to 7 larvae ml^{-1}. Mean shell length of *G. gemma* was 2.4 mm. *Significantly higher than the control at $0.01 < p < 0.05$; #: significantly higher than the low *G. gemma* density treatment at $0.01 < p < 0.05$. See Table 1 for size, age and concentration of the larvae and duration of exposure in each trial

the size of *Gemma gemma*. Settlement was assessed for 0, 50 and 200 gravel particles in each well. Clean sand was used as a substrate. Gravel particles were collected from Flax Pond and ignited at 550 °C for 5 h. Gravel particles were mixed through the burrowing depth (~ 5 mm) of gem clams to simulate, at least initially, presence of gem clams in sediment. Experimental design was otherwise like Expt 1.

Expt 7: response to gem clam shells: The purpose of this experiment was to determine the effect of physical and chemical presence of gem clams on larval settlement of hard clams. Settlement was assessed in sand with 0, 50 and 200 empty *Gemma gemma* shells (2.4 mm mean length) in each well. Empty shells were prepared by soaking in 30 % H_2O_2 for 24 h and rinsing thoroughly with distilled water. Shells were mixed through the burrowing depth of gem clams to simulate the presence of gem clams in sediment. Control sediments were not mixed. Experimental design was otherwise like Expt 1.

RESULTS

Expt 1 demonstrated that *Gemma gemma* enhanced *Mercenaria mercenaria* larval settlement. In 3 of the 4 trials, dense gem clam patches enhanced settlement of hard clam larvae (Fig. 1). Low *G. gemma* density enhanced settlement only in Trial 4. In none of the trials did presence of *G. gemma* reduce larval settlement, and only in Trial 3 was the *G. gemma* effect not significant. Larvae used in Trial 3 were slightly larger than those used in the other trials (Table 1), and they may have settled too rapidly for habitat selection to occur. They settled within 24 h after introduction, while in the other trials they swam for at least 48 h before settling.

In Expt 2, dense patches of gem clams enhanced settlement of hard clam larvae in both recirculated water and gently aerated water (Fig. 2). Settlement response was similar in these 2 different water regimes; an order of magnitude more larvae settled in presence of *Gemma gemma* than in their absence.

Table 1. Expt 1. Size, age, and concentration of *Mercenaria mercenaria* larvae used, and duration of exposure of larvae to experimental treatments in 4 consecutive settlement trials

	Trial no. 1	2	3	4
Shell size (mean length in µm)	190	189	200	171
Age (d)	11	9	9	8
Concentration (larvae ml^{-1})	4	6	7	6
Duration of exposure (h)	52	72	48	53

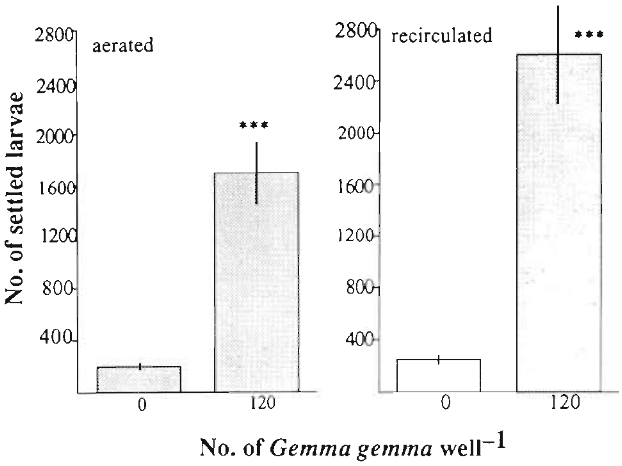

Fig. 2. Expt 2. Effect of *Gemma gemma* on settlement of *Mercenaria mercenaria* in gently aerated and recirculated (by airlifting) waters. Mean (± 1 SE) no. of settled larvae (n = 3). Larvae were exposed to treatment for 3 d. Treatments were conducted during the same period using the same batch of larvae. Mean shell length of larvae was 177 µm (11 d old). Larval concentrations in 7 l tank were ~4 larvae ml^{-1} in recirculated water and ~3 larvae ml^{-1} in aerated water. Mean shell length of *G. gemma* was 2.9 mm. ***Significantly ($p < 0.001$) higher than the control

Expt 3 showed that dense patches of *Gemma gemma* enhanced settlement of hard clam larvae in sand and muddy sand (Fig. 3). For each *G. gemma* density, there was no significant difference in the number of larvae that settled in sand and muddy sand.

In Expt 4, settlement of hard clam larvae was enhanced in the presence of high densities of *Gemma gemma* and juvenile *Mercenaria mercenaria* (Fig. 4). There was no significant difference in larval settlement among any of the juvenile hard clam or gem clam treatments. However, all clam treatments differed from the control.

Expt 5 demonstrated that *Mercenaria mercenaria* larvae preferentially settled in sand previously exposed to gem clams, and that settlement increased with *Gemma gemma* exposure density (Fig. 5).

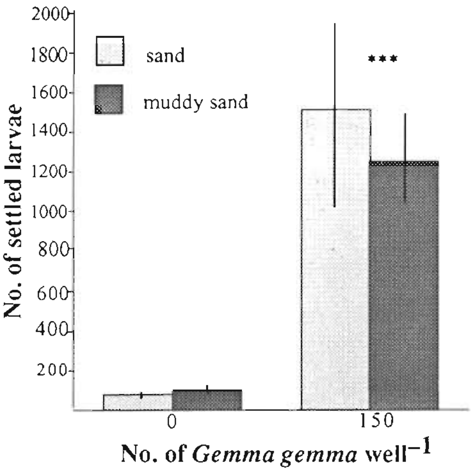

Fig. 3. Expt 3. Effect of *Gemma gemma* on settlement of *Mercenaria mercenaria* in clean sand and muddy sand. Mean (± 1 SE) no. of settled larvae (n = 3). Larvae were exposed to the treatment for 3 d. Mean larval shell length was 177 µm (11 d old) and larval concentration in the 19 l tank was ~3 larvae ml^{-1}. Mean shell length of *G. gemma* was 2.5 mm. ***Significantly ($F_S = 146.55$, $p < 0.001$) higher settlement in presence of gem clams than in its absence in both sediment types, there was no significant difference between 2 sediment types

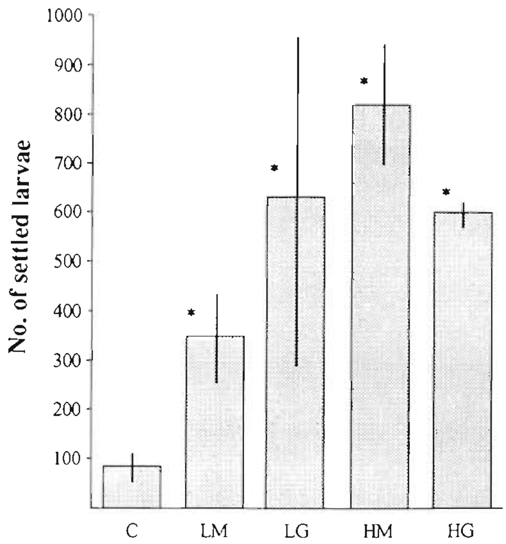

Fig. 4. Expt 4. Settlement of *Mercenaria mercenaria* larvae in response to juvenile *M. mercenaria* and gem clams *Gemma gemma* of the same size (3 mm mean shell length). Larvae were exposed to treatments for 3 d. Mean shell length of larvae was 174 µm (11 d old) and concentration in the 7 l tank was ~2 larvae × ml^{-1}. C: control, without juvenile *M. mercenaria* or *G. gemma*. LM: low density (27 clams well^{-1}) of juvenile *M. mercenaria*, HM: high density (110 clams well^{-1}) of *M. mercenaria*, LG: low density of *G. gemma*, HG: high density of *G. gemma*. *Significantly ($0.01 < p < 0.05$) different from control, no significant difference among any juvenile hard or gem clam treatments

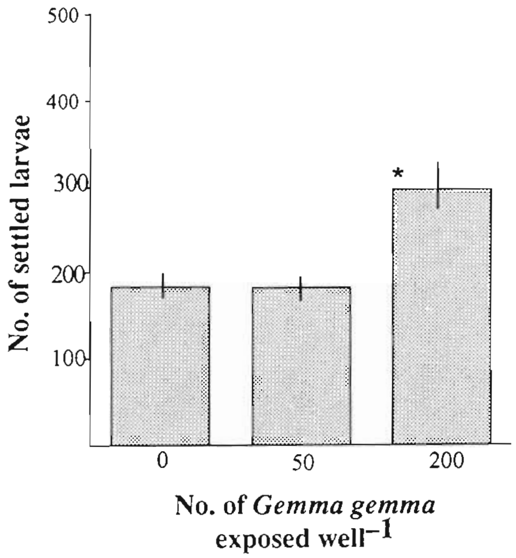

Fig. 5. Expt 5. Settlement of *Mercenaria mercenaria* larvae in response to sediment exposed to *Gemma gemma*. Mean (± 1 SE) no. of settled larvae. *G. gemma*-exposed sediment was prepared by placing gem clams in sediment wells for 3 d. Gem clams were picked out just before introduction of hard clam larvae. Mean shell lengths: *M. mercenaria*, 174 µm (8 d old); *G. gemma*, 2.4 mm. Larval concentration in 7 l tanks was ~2 larvae ml^{-1}. *Significantly different than control and low treatments at $0.01 < p < 0.05$

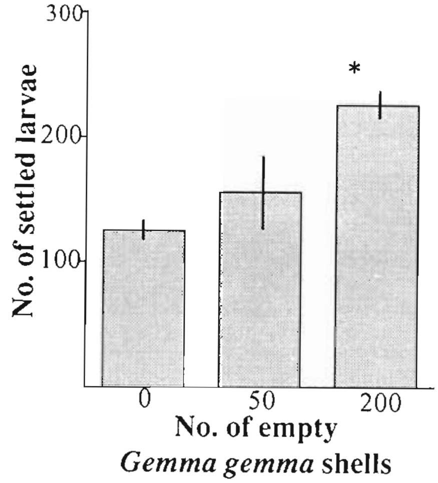

Fig. 7. Expt 7. Settlement of *Mercenaria mercenaria* larvae in response to *Gemma gemma* shells. Mean (± 1 SE) no. of larvae settled (n = 4) per well. Experiment was run for 3 d. Mean shell length of larvae was 174 µm (11 d old) and concentration of larvae in 7 l tank was ~2 larvae ml^{-1}. Mean shell length of G. gemma was 2.4 mm. *Significantly ($0.01 < p < 0.05$) different from control and low *G. gemma*-shell density treatment

In Expt 6, addition of gravel particles did not enhance larval settlement (Fig. 6). In contrast, Expt 7 established that adding a high concentration of empty *G. gemma* shells to sand did enhance settlement of hard clam larvae (Fig. 7).

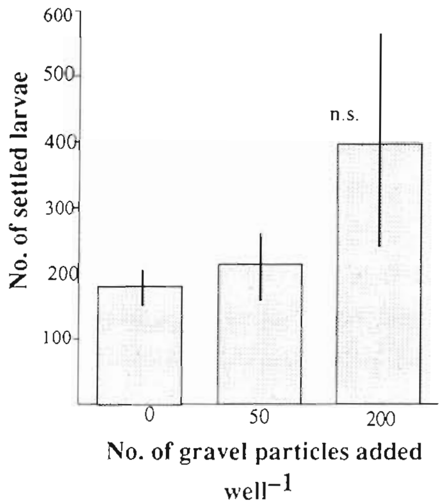

Fig. 6. Expt 6. Settlement of *Mercenaria mercenaria* larvae in response to presence of gravel particles. Particles of 2 to 3 mm diameter were similar in size to adult *Gemma gemma*. Larvae were exposed to treatment for about 3 d

DISCUSSION

In contrast to assertions that dense assemblages of suspension feeders should diminish larval settlement, dense patches of *Gemma gemma* could enhance larval settlement of *Mercenaria mercenaria* (Figs. 1 to 3). Settlement tended to increase with increasing density of gem clams within the density range tested (Fig. 1). Since siphonal diameter in gem clams is only slightly larger than hard clam larvae (less than twice the larval length), it is unlikely that hard clam larvae were ingested or filtered by gem clams. Woodin (1976) contended that even for larvae too large to be ingested, entrapment in pseudofeces is probably often fatal. However, microscopic examination showed that settled larvae were crawling or burrowing, and enhanced settlement did not result from trapping or entanglement of *M. mercenaria* larvae in the sticky fecal material produced by *G. gemma*. It is apparent that *M. mercenaria* larvae preferentially settled on sediment with *G. gemma* and that exclusion of *M. mercenaria* larvae by adult *G. gemma* did not occur during settlement.

The high gem clam density used in these experiments, 200 clams well^{-1} (= 2×10^5 m^{-2}) was close to the highest densities ever reported for *Gemma gemma* populations (Bradley & Cooke 1959, Sanders et al. 1962, Sellmer 1967, Green & Hobson 1970, Thomson 1982). At this density, the sediment surface in experimental wells was initially completely covered with clams, rather like a cobblestone street. However, many gem clams started to burrow into the sediment within a few minutes, leaving some space at the surface. Also, many hard clam larvae burrowed partially or completely after settlement. The 3-dimensionality of sediment might permit some vertical segregation, in particular microscale differentiation of living and/or feeding depth (Peterson 1979, Peterson & Andre 1980, Elmgren et al. 1986). Thus competitive interactions between hard clam larvae and established gem clams may be less intense than anticipated.

Preferential settlement due to gem clams in both aerated water and recirculated water (Fig. 2) suggests that hard clam larvae could recognize settlement cues even in presence of 1 sort of flow. An alternative interpretation is that selection is entirely post-depositional (Luckenbach 1984, Woodin 1986), although use of discrete, elevated 'islands' of sediment in our experiments renders this interpretation less likely. In stronger flow regimes than used in these experiments, hard clam larvae are not be able to select their habitats and are deposited like passive particles (Butman et al. 1988). Butman et al. (1988) also discussed the role of competency on settling rates of *Mercenaria mercenaria* larvae. Since larval concentrations in the 2 water regimes were slightly different, it is difficult to determine whether water regime affected hard clam larval settlement.

Consistent preferential settlement in the presence of gem clams in both sand and muddy sand (Fig. 3) suggests that larvae recognize settlement cues associated with *Gemma gemma* in various habitats. Other studies have shown that *Mercenaria mercenaria* larvae preferentially settle on low-organic sand or glass beads rather than organically rich mud (Keck et al. 1974, Butman et al. 1988); they used pure mud while we used a 10 % (w/w) mud/sand mixture. It is reasonable that larvae of suspension-feeding bivalves choose low-organic sand because it is indicative of substantial water motion and therefore constant renewal of suspended food (Sanders 1958, Butman et al. 1988). Nevertheless, in this study *M. mercenaria* larvae settled well on muddy sand when it was occupied by *G. gemma*.

The fact that *Mercenaria mercenaria* larvae settled in response to gem clams raised questions of whether they show a similar settlement response to their own species and whether the response to conspecific juveniles is stronger than response to adult *Gemma gemma*. In fact, juvenile *M. mercenaria* and adult *G. gemma* had the same effect on settlement of *M. mercenaria* larvae (Fig. 4). Considering that juvenile *M. mercenaria* and adult *G. gemma* are similar in size, shape, burrowing depth, and feeding behavior, it is reasonable to suggest that *G. gemma* and juvenile *M. mercenaria* facilitate settlement of hard clam larvae in similar ways. The fact that conspecifics were not more attractive suggests that a specific settlement cue was not involved.

Enhanced settlement of *Mercenaria mercenaria* larvae on *Gemma gemma*-exposed sand (Fig. 5) implies that enhanced larval settlement in presence of gem clams may have been at least partly due to sediment alteration resulting from gem clam activities. This may indicate presence of biochemical substances produced by gem clams that are settlement cues. Alternatively, enhanced pore water and particle flux due to clam movement, ventilation and feeding could alter the microbial flora in sediment (Weinberg & Whitlatch 1983, Aller & Yingst 1985), although use of clean sand would tend to minimize microbial activities. Biodeposits, especially pseudofeces, may be an attractive settlement cue in a way that other sedimentary organic matter is not. In addition, the fact that both gravel particles tended to, (Fig. 6) and empty *G. gemma* shells (Fig. 7) did, enhance *M. mercenaria* settlement, suggests that physical factors such as differences in sediment texture, roughness and grain size of sediment are also important agents in stimulating settlement. Several settlement cues may be operating in these experiments.

In summary, this study demonstrates for the first time that dense assemblages of small suspension feeders enhance larval settlement of another species. These results are surprising in light of observations that other bivalves do not co-occur with dense populations of *Gemma gemma* (Sanders et al. 1962, Green & Hobson 1970). We would not have been particularly surprised if gem clams did not affect larval settlement. Other studies have shown that even large suspension feeders either do not reduce larval settlement (e.g. Maurer 1983, Hunt et al. 1987, Black & Peterson 1988, Young 1989, 1990), or if reduced, substantial numbers still settle (Williams 1980, Peterson 1982, Hines et al. 1989). Finding a consistent, density-dependent enhancement of larval settlement suggests that negative interactions between adult suspension feeders and planktonic larvae are only part of the story. Our results are particularly intriguing in light of a companion study demonstrating that dense assemblages of *Gemma gemma* enhance survival, growth and migration of early post-larval stages of *Mercenaria mercenaria* (Ahn et al. 1993).

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