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# Effects of the gem clam *Gemma gemma* on early post-settlement emigration, growth and survival of the hard clam *Mercenaria mercenaria*

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ABSTRACT: The purpose of this study was to determine the effects of dense patches of adult *Gemma gemma*, food concentration, and substrate type on emigration, growth and survival of newly settled *Mercenaria mercenaria*. Hard clams emigrated more in the presence of *G. gemma* than in its absence in both laboratory and field experiments. The overall effect of reduced food was increased emigration. Presence of *G. gemma* in sand enhanced hard clam growth while not affecting survival, but in muddy sand growth and survival decreased. Hard clams grew best in muddy sand without gem clams. In further experiments hard clams grew faster in shallower sediments and slower with addition of *G. gemma* biodeposits. We conclude that undisturbed post-settlement *M. mercenaria* grow more slowly than they are capable of because they spend part of the time buried, presumably to avoid surface predators. Clams that are kept near the sediment surface, either because of sedimentary properties or interaction with spatial competitors, grow considerably faster than undisturbed clams in sand. This interpretation implies a trade-off between opposing selective pressures such that clams partition time between the necessary risk of feeding and the safe but energetically unprofitable sub-surface refuge from predation.

## INTRODUCTION

Established benthos may affect the early recruitment of benthic animals through ingestion or filtration of larvae, sediment reworking, competition and predation. Woodin (1976) predicted that inhibition of larval recruitment by adult organisms in the sediment is an important mechanism in controlling soft-bottom community structure. Experimental studies demonstrated that resident adults negatively impact settling and newly settled infauna (Williams 1980, Wilson 1980, Brenchley 1981, Levin 1981, Peterson 1982, Gallagher et al. 1983, Luckenbach 1984, Tamaki 1985, Woodin 1985).

In this study we investigated the effect of gem clams *Gemma gemma* on newly settled hard clams *Mercenaria mercenaria*. The gem clam, a small (5 mm) suspension-feeding bivalve, is one of the most abundant infaunal species in shallow estuarine benthos (Bradley & Cooke 1959, Sanders et al. 1962, Sellmer 1967, Green & Hobson 1970, Maurer et al. 1978, Woodin 1981, Thomson 1982, Botton 1984). Adult populations often reach summer densities of $10^5$ ind. $m^{-2}$ (Bradley & Cooke 1959, Sanders et al. 1962, Sellmer 1967, Green & Hobson 1970, Thomson 1982). It shares with *M. mercenaria* much of the same habitat and geographic range. It is morphologically similar, particularly in siphonal structure, to newly settled hard clams and feeds mostly at the sediment-water interface (Sellmer 1967). Bradley & Cooke (1959) and Sanders et al. (1962) observed an inverse relationship between abundances of *G. gemma* and other suspension-feeding bivalves, and suggested that dense *G. gemma* populations inhibit recruitment of other suspension feeders by outcompeting the tiny spat for food.

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Ahn et al. (1993) demonstrated in laboratory experiments that *Mercenaria mercenaria* larvae preferentially settled in dense patches of gem clams. Considering the close taxonomic affinity and similarities in shape, living depth and feeding type, competition for food or space might occur between newly settled hard clams and adult gem clams following settlement.

Unlike juvenile or adult hard clams, which reside deeply in sediment with siphons exposed at the sediment surface, newly settled hard clams are asiphonate, so suspension-feeding is restricted to surface sediment, or shallow pore water in porous sediment (Carriker 1961). Hence feeding exposes them to epibenthic predators and environmental stresses. Until siphons fully develop, hard clams spend their time alternating between byssal attachment and crawling. Rivara (1985) observed that juvenile hard clams up to 1 mm burrowed into sediment at the onset of illumination, but remained at the surface in darkness. Negative phototaxis may be a remnant of a larval adaptation, but this response may help control trade-offs between surface feeding and sub-surface avoidance of predators. We investigate here how biotic and environmental factors modulate this trade-off.

The present study investigated interactions between newly settled hard clams and adult gem clams. The effects of a dense gem clam population on emigration, growth and survival of newly settled hard clams were determined, and differential *Gemma gemma* effects on post-settlement processes of hard clams between substrates were demonstrated.

## MATERIALS AND METHODS

*Mercenaria mercenaria* larvae were obtained from a hatchery company (Bluepoints Co., Inc.) and cultured until they metamorphosed (200 µm length at settlement) (Loosanoff 1959). *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 hard and gem clams were allowed to acclimate to experimental conditions for at least 3 d. Both bivalve species were fed on *Isochrysis galbana* (clone T-iso; 4 µm) during acclimation and experimental periods.

Clean, medium-sized (250 to 500 µm) sand and muddy sand (10 mud:90 sand, w·w) were used as substrates. Sediment was prepared as described in Ahn et al. (1993).

Experimental conditions in the laboratory were similar to early summer conditions in Great South Bay with respect to illumination, temperature and salinity. See Ahn et al. (1993) for added details. Unless otherwise stated, seawater was filtered through 0.2 µm cartridge filters.

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 on a 1 mm sieve and hard clams were extracted by mixing and decantation. Ahn et al. (1993) describes methods in more detail.

ANOVA and multiple comparisons among means (Sokal & Rohlf 1981) were used to test statistical significance of experimental factors. Assumptions for ANOVA were tested and transformations were employed where appropriate.

**Emigration Expt 1: effects of *Gemma gemma*, sediment type and food concentration.** In preliminary experiments, recovery of hard clams varied with experimental treatments. Apparently, a number of hard clams emigrated from where they were initially transplanted. In this experiment, we determined the effects of a dense *G. gemma* population, sediment type and food concentration on emigration of newly settled *Mercenaria mercenaria*.

The experiment was conducted in a 38 l glass aquarium filled with seawater to a depth of 15 cm. Water was recirculated constantly at 2 l $min^{-1}$ by airlifting (Kinne 1976) through 2 L-shaped PVC tubes at diagonally opposite corners; turnover time was 9.5 min.

Treatments consisted of sand or muddy sand with 0 or 70 gem clams 5.5 $cm^{-2}$; each combination was run at 2 food concentrations (1 to 2 $\times$ $10^4$ and 0.5 to 1 $\times$ $10^5$ cells $ml^{-1}$). Each treatment was kept in a separate petri dish (6 cm diameter, 1 cm depth) modified to estimate emigration rates. A plastic cylindrical well (2.65 cm diameter and 2 cm height) was glued to the center of each petri dish. Each well was filled up to the rim with prepared sediment. The rest of the dish was covered with a 2 mm layer of sand. Three replicates of each treatment were then placed in the aquarium in a completely randomized design.

Gem clams were placed into the cylinders. Approximately 24 h later, 200 hard clams (259 µm in mean shell length) were put into each cylinder. The experiment ran for 1 wk, then sediment was collected both from cylinders and surrounding areas in petri dishes, and retrieved hard clams were counted. Preliminary observations determined that hard clams which dropped from cylinders into petri dishes did not climb up. Emigration rate was expressed as percentage of clams collected from the surrounding area of the total retrieved.

**Emigration Expt 2: effect of *Gemma gemma* in the field.** The effect of *G. gemma* patches on *Mercenaria mercenaria* emigration was tested in Flax Pond, 6 to 9 September 1989. We measured movement of post-settlement hard clams from sieved (< 1 mm) Flax Pond

sediment with 0 or 120 *G. gemma* 10 $cm^{-2}$. The sediment was a muddy sand mixed with shell fragments.

Three replicates for each treatment were prepared in cubical freezer boxes ($10^3$ $cm^3$). A small cylindrical cage (10 $cm^2$, 5 cm high) of 1.6 mm mesh Nytex was pushed halfway into each freezer box; cages prevented *Gemma gemma* from emigrating but allowed *Mercenaria mercenaria* to move freely in and out of the cage. For the gem clam treatment, 120 *G. gemma* were placed within each appropriate cage and were allowed to acclimate in a flowing seawater system for 24 h. Then 250 newly (a few days after settlement) metamorphosed hard clams (264 µm mean shell length) were pipetted inside each cage. Freezer boxes were then placed into a holding table in a completely randomized design (2 × 3 array). The table was covered by a Nytex screen (1.6 mm mesh) to exclude small predators such as *Crangon septemspinosa*, and placed in a metal cage (1 cm mesh) to exclude larger predators such as mud crabs.

The table was kept 10 cm off bottom to reduce sedimentation. The cage was placed in a shallow subtidal channel. Water depth at low tide was about 5 cm above freezer boxes, and tidal range was about 1.6 m. Freezer boxes were retrieved after 3 d, and the top 1 cm of sediment was collected from Nytex cages and preserved. The effect of *Gemma gemma* on the emigration rate of newly metamorphosed *Mercenaria mercenaria* was measured.

**Growth Expt 1: effects of densities.** Effects of *Gemma gemma* and *Mercenaria mercenaria* densities on growth and survival of early post-settlement *M. mercenaria* were tested. This experiment was run twice, one trial using a high food level, the other with low food. Since there was seasonal variation in size of adults (2.4 to 3.0 mm in mean shell length), the number of *G. gemma* for low (27 to 50 clams $well^{-1}$) and high (110 to 200 clams $well^{-1}$) density treatments was determined on the basis of total wet weight (low: 25 mg $cm^{-2}$; high: 100 mg $cm^{-2}$). These densities were well within the natural range (Bradley & Cooke 1959, Sanders et al. 1962, Sellmer 1967, Green & Hobson 1970, Thomson 1982).

The trials were conducted in a glass aquarium as described earlier, except that aeration was from airstones from 4 sides. Eight multi-well plates (12.7 × 8.5 × 1.7 cm) were filled with clean sand. Each plate consisted of 6 wells (3.6 cm diam., 1 cm depth).

Growth and survival of hard clams were assessed at zero, low and high *Gemma gemma* densities (see above). Gem clams were transplanted into wells and allowed to acclimate to experimental conditions. Three replicates for each treatment were placed in wells in a completely randomized design, and plates were then placed in the aquarium. Twenty-four hours later, newly metamorphosed hard clams were pipetted into wells at densities of 50, 200 and 1000 clams $well^{-1}$. Seawater was changed every other day throughout the 2 wk experimental period. The first trial ran all *G. gemma* × *Mercenaria mercenaria* combinations at a low food level (1 to 2 × $10^4$ T-iso cells $ml^{-1}$) and the second trial used a high algal concentration (0.5 to 1 × $10^5$ T-iso cells $ml^{-1}$).

Size of hard clams was determined with an optical pattern recognition system (Biosonics, Inc.). Mean initial shell lengths were identical among treatments. Final shell lengths were used as a measure of growth. At the end of each experiment minimum sample sizes for unbiased sample means were determined (Cochran 1963, p. 77). Minimum samples were taken from each replicate for measurement of shell length. Survival rate was expressed as percentage of clams alive at the end of an experiment to total clams retrieved.

**Growth Expt 2: effects of density and sediment type.** The purpose of this experiment was to evaluate separate and combined effects of *Gemma gemma* density and sediment type on *Mercenaria mercenaria* growth. Experimental design was similar to Expt 1. Two *G. gemma* densities were used, 0 and 120 clams $well^{-1}$. Each density was tested in sand and muddy sand.

**Mechanism Expt 1: effect of sediment thickness.** Based on the results of the growth experiments, we conducted several additional experiments to elucidate mechanisms. This experiment was conducted to determine the effects of sediment thickness on hard clam growth. Sediments of different thickness were used to simulate differences in sediment chemistry caused by physical activities of *Gemma gemma*. Irrigation activity of macrofauna can increase pore water exchange with overlying water, and remove inhibitory metabolites from the sediment (Aller 1982). In a thin sediment layer, pore water equilibrates easily with overlying water, thus it is analogous to a well-irrigated sediment (R. Aller pers. comm.). Thicker sediment layers have gradients of metabolites in the pore water.

A thin sediment layer also constrains the burrowing depth of hard clams; clams in a thin layer are kept near the surface while animals in a thicker layer can burrow.

*Mercenaria mercenaria* growth was assessed in sediment layers of 3 mm, 1 cm and 3 cm depth. Cylindrical PVC containers were filled to appropriate depths with clean sand. Four replicates for each sediment thickness were then placed in a Plexiglas container in a completely randomized design (3 × 4 array). Seawater was aerated and changed every other day over a 2 wk period. Algal food was provided (0.5 to 1 × $10^5$ T-iso cells $ml^{-1}$). This experiment was conducted twice.

**Mechanism Expt 2: retention efficiencies of algae and biodeposits.** This experiment was run to test

whether *Gemma gemma* biodeposits are used as food by newly settled hard clams. $^{14}$C-labeled algae were prepared by growing *Isochrysis galbana* in presence of $^{14}$C-bicarbonate (1 µCi ml$^{-1}$ culture) for 5 d at 20 °C under constant illumination. Labeled cells were harvested and cleaned by centrifugation 3 to 4 times (4000 rpm, or 3000 × *g*, for 15 min each time), and resuspended in unlabeled seawater.

A total of 150 *Gemma gemma* (3 mm) were fed $^{14}$C-labeled algae (5 to 6 × 10$^5$ cells ml$^{-1}$) for 40 min, then were transferred to unlabeled algae at the same concentration. After 1 h gem clams were removed. $^{14}$C biodeposits, produced by clams feeding on labeled algae, were concentrated on a 1.0 µm Nuclepore membrane filter, and then resuspended in 50 ml seawater. The biodeposit suspension was divided into 5 aliquots (10 ml each), 1 for measurement of $^{14}$C loss and 4 for feeding to hard clams.

For measuring retention of biodeposits, 4 groups of 100 *Mercenaria mercenaria* (350 µm mean shell length) were placed in beakers of unlabeled algae. Aliquots of biodeposit suspensions were then added and hard clams were allowed to eat for 40 min. Algal depletion during the feeding experiment was less than 5 % of initial concentration. Then clams were transferred to beakers of unlabeled algae. Subsequent transfers were made every 2 h for 8 h. After each transfer, algae and feces were collected separately on glass fiber filters. The experiment was conducted at 23 °C.

Algal absorption by post-settlement *Mercenaria mercenaria* was measured using similar protocol. Eight groups of 80 hard clams (498 µm mean shell length) were fed labeled algae. Labeling method and experimental procedure were as described above.

Filters and clams were placed in LSC vials and 10 ml scintillant (Scintiverse II, Fisher) was added. Samples were eluted for 3 d before counting. $^{14}$C activity was estimated by liquid scintillation (LKB-Wallac 1217), using external standards quench correction. Because $^{14}$C-DOC was not estimated, retention efficiency was calculated as a conservative measure of absorption efficiency. Retention efficiency was calculated as the ratio of $^{14}$C retained in clams to the total $^{14}$C defecated and retained in clams.

**Mechanism Expt 3: effect of biodeposits.** This experiment was conducted to determine whether biodeposits affect hard clam growth. Growth of newly settled *Mercenaria mercenaria* was assessed for the following treatments: (1) no biodeposits; (2) 0.1 to 0.2 mg dry wt biodeposits d$^{-1}$ (produced by 25 gem clams, 3 mm); (3) 0.4 to 0.8 mg dry wt biodeposits d$^{-1}$ (produced by 100 gem clams). Each treatment was added to a 250 ml beaker having 2 mm layer of sand and 200 ml aerated seawater. Two hundred newly metamorphosed hard clams (257 µm mean shell length) were pipetted into each beaker.

Each day, biodeposits were collected on a 20 µm sieve (70 % of particles were 20 to 30 µm) from gem clams and added to the beakers. Gem clams were fed 0.5 to 1 × 10$^5$ cells ml$^{-1}$ T-iso. Prior to daily addition of biodeposit, 75 % of the seawater was changed using a siphon to avoid disturbing sediment. Hard clams were provided with 0.5 to 1 × 10$^5$ cells ml$^{-1}$ T-iso as a primary food source over the 2 wk experimental period.

## RESULTS

### Emigration

In Emigration Expt 1, presence of gem clams increased hard clam emigration under both high and low food concentrations (Fig. 1). In their absence, >95 % of hard clams remained within the cylinders. More emigration occurred in muddy sand than in sand under high food concentration, and overall emigration rates were significantly higher under low than under high food concentration (Fig. 1). Interaction between *Gemma gemma* and Food was highly significant (Table 1). Other treatment interactions (*G. gemma* × Sediment, Sediment × Food, and *G. gemma* × Sediment × Food) were not significant (Table 1). Survival was high (>97 %), and there was <1 % difference in survival between migrators and non-migrators. From 87.3 to 96.7 % of the hard clams were retrieved from

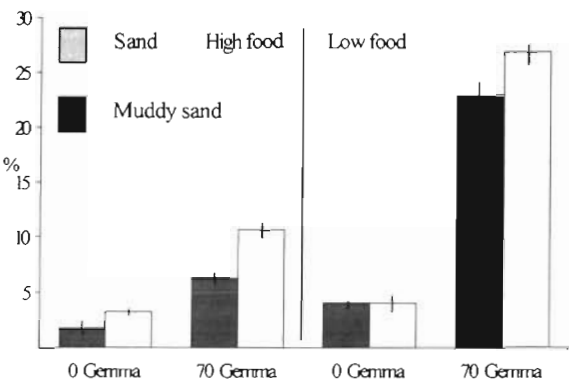


Fig. 1 Emigration Expt 1. Effects of *Gemma gemma*, sediment type and food concentration on emigration of newly settled *Mercenaria mercenaria*. Means (±1 SE) of emigration rates for 3 replicate samples. Emigration is measured as percent of initial number of hard clams (200) that moved out of cylinders. Food concentration: high, 0.5 to 1 × 10$^5$ cells ml$^{-1}$; low, 1 to 2 × 10$^4$ cells ml$^{-1}$ Mean initial shell lengths: *M. mercenaria*, 259 µm; *G. gemma*, 2.8 mm. There was higher migration in the presence of gem clams at both food concentrations. Under high food, there was more ($p < 0.01$) migration in muddy sand than in sand. See Table 1 for ANOVA results

Table 1. Emigration Expt 1. Three-way ANOVA table for the effects of *Gemma gemma*, sediment type and food concentration on emigration rate of newly settled *Mercenaria mercenaria*. •••$p < 001$; ••$0.001 < p < 0.01$; ns: not significant

| Source | SS | df | MS | $F_S$ | |
|---|---|---|---|---|---|
| *G. gemma* | 1090.53 | 1 | 1090.53 | 226.35 | ••• |
| Sediment | 43.63 | 1 | 43.63 | 9.06 | •• |
| Food | 489.79 | 1 | 489.79 | 101.66 | ••• |
| *G. gemma* × Sediment | 21.36 | 1 | 21.36 | 4.43 | ns |
| *G. gemma* × Food | 323.99 | 1 | 323.99 | 67.25 | ••• |
| Sediment × Food | 0.93 | 1 | 0.93 | 0.19 | ns |
| *G. gemma* × Sediment × Food | 0.41 | 1 | 0.41 | 0.08 | ns |
| Error | 77.09 | 16 | 4.82 | | |

Table 2. Emigration Expt 1. Effect of *Gemma gemma*, sediment type and food concentration on recovery of *Mercenaria mercenaria*. Recovery efficiency of hard clams: total percent recovered (cylinder and petri dish) of initial 200 added. Means (± SD), n = 3. Initial shell lengths: *M. mercenaria*, 259 µm; *G. gemma*, 2.8 mm. Retrieval rates were significantly lower in presence of *G. gemma* (3-way ANOVA: $F_S = 10.938$, $p < 0.01$)

| Sediment type | *G. gemma* cylinder$^{-1}$ 0 | 70 |
|---|---|---|
| **High food concentration (0.5 to 1 × $10^5$ cells ml$^{-1}$)** | | |
| Sand | 90.0 (6.50) | 87.3 (6.17) |
| Muddy sand | 96.3 (2.93) | 89.0 (0.87) |
| **Low food concentration (1 to 2 × $10^4$ cells ml$^{-1}$)** | | |
| Sand | 92.2 (2.57) | 87.7 (4.62) |
| Muddy sand | 96.7 (0.76) | 88.5 (4.77) |

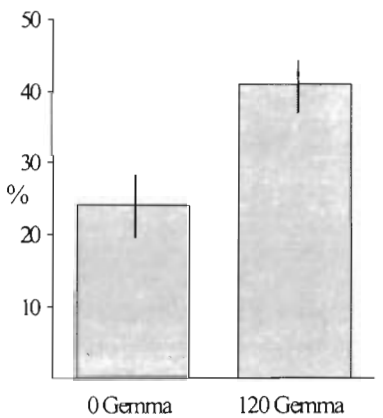


Fig. 2. Emigration Expt 2. Effect of *Gemma gemma* density on emigration of newly settled *Mercenaria mercenaria* in a 3 d field experiment. Means (± 1 SE) of migration rates for 3 replicate samples. Migration rate presented as percent of initial hard clams (250 per plot) that left their plot. *G. gemma* densities are per 10 cm$^2$. Mean shell length of *M. mercenaria* was 264 µm, for *G. gemma* 2.9 mm. $F_S = 6.6319$ ($p < 0.10$)

both cylinders and the rest of the petri dish. For reasons not understood, significantly fewer hard clams were retrieved from treatments containing gem clams (Table 2).

In Emigration Expt 2, the presence of *Gemma gemma* did not increase *Mercenaria mercenaria* emigration rate (Fig. 2). Emigration rates were higher in this field experiment than in the previous laboratory experiment.

## Growth

Growth Expt 1 demonstrated that the presence of gem clams enhanced hard clam growth at both low and high algal concentrations (Fig. 3a, b). Multiple comparisons among means (Welsch step-up procedure) showed that growth rate increased with increas-

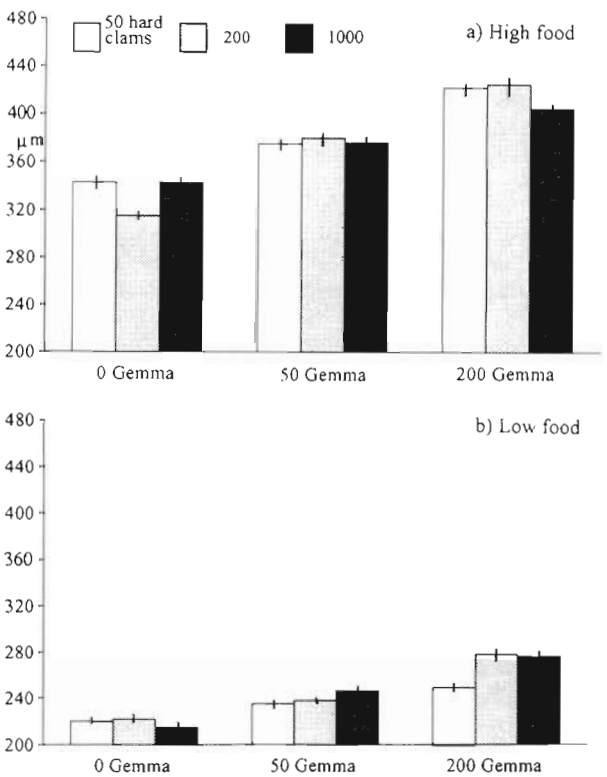


Fig. 3. Growth Expt 1. Effects of *Gemma gemma* and *Mercenaria mercenaria* densities on growth of newly settled *M. mercenaria*. Means (± 1 SE) of final shell lengths are shown. Samples were pooled from 3 replicates. *M. mercenaria* density ranged from 50 to 1000, *G. gemma* from 0 to 200. (a) High food treatment; mean initial shell length of *M. mercenaria* was 225 µm (± 3.0 SE). (b) Low food, mean initial shell length of *M. mercenaria* was 200 µm (± 2.1 SE). Mean shell length of *G. gemma* was 2.4 mm. See Table 3 for ANOVA

Table 3. Growth Expt 1. Two-way ANOVA tables for the effects of *Gemma gemma* density, *Mercenaria mercenaria* density, and interaction for high and low food concentrations. •••p < 0.001; ns: not significant

| Source | SS | df | MS | $F_S$ | |
|---|---|---|---|---|---|
| **High food concentration (0.5 to 1 × $10^5$ cells $ml^{-1}$)** | | | | | |
| *M. mercenaria* | 5 705 | 2 | 2 853 | 1.43 | ns |
| *G. gemma* | 939 453 | 2 | 469 727 | 236 | ••• |
| *M. mercenaria* × *G. gemma* | 52 234 | 4 | 13 059 | 6.55 | ••• |
| Error | 1 595 999 | 801 | 1 993 | | |
| **Low food concentration (1 to 2 × $10^4$ cells $ml^{-1}$)** | | | | | |
| *M. mercenaria* | 26 023 | 2 | 13 011 | 13.5 | ••• |
| *G. gemma* | 366 651 | 2 | 183 326 | 189.8 | ••• |
| *M. mercenaria* × *G. gemma* | 1 516 | 4 | 379 | 0.4 | ns |
| Error | 790 350 | 818 | 966 | | |

Table 4. Growth Expt 1. Effects of intra- and inter-specific *Gemma gemma* and *Mercenaria mercenaria* densities and food concentration on survival of newly settled *M. mercenaria*. Survival is expressed as percentage of living clams of the total number of clams at the end of the experiment. Means (SD) for 3 replicate samples

| *M. mercenaria* 10 $cm^{-2}$ | *G. gemma* 10 $cm^{-2}$ | | |
|---|---|---|---|
| | 0 | 50 | 200 |
| **High food concentration (0.5 to 1 × $10^5$ cells $ml^{-1}$)** | | | |
| 50 | 98.7 (2.19) | 98.8 (1.06) | 98.7 (1.10) |
| 200 | 97.0 (1.05) | 98.5 (0.42) | 99.0 (0.36) |
| 1000 | 97.5 (1.46) | 99.5 (0.00) | 99.1 (0.26) |
| **Low food concentration (1 to 2 × $10^4$ cells $ml^{-1}$)** | | | |
| 50 | 73.9 (6.22) | 77.3 (0.87) | 71.6 (5.35) |
| 200 | 74.0 (10.2) | 87.1 (6.31) | 88.0 (2.49) |
| 1000 | 65.0 (10.2) | 73.5 (10.8) | 83.5 (1.38) |

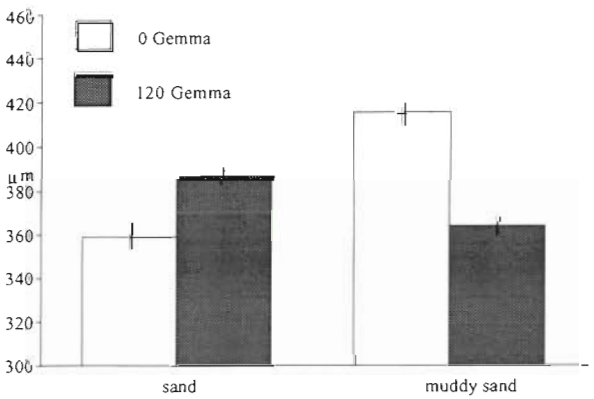


Fig. 4. Growth Expt 2. Effect of *Gemma gemma* density and sediment type on growth of newly settled *Mercenaria mercenaria*. Algal food was at 0.5 to 1 × $10^5$ cells $ml^{-1}$ over a 2 wk experimental period. Means (± 1 SE) of final shell length (µm) for 3 replicate samples (n = 120; 40 from each replicate). Initial mean shell length of hard clams was 226 (± 2.86 SE) µm, of *G. gemma*, 2.9 mm. See Table 5 for ANOVA

ing density of gem clams in both low and high food levels. There was no intra-specific density effect for *Mercenaria mercenaria* under high food. There was an intra-specific density effect (Table 3, 2-way ANOVA: $F_S$ = 13.466, $p < 0.001$) at lower food, although multiple comparisons among means showed no significant intraspecific density effects within the density range tested. There was a significant *Gemma gemma* × *Mer-cenaria mercenaria* interaction in the high food trial, but not under low food (Table 3).

Survival rates in the high food trial were very high, ranging from 97.0 to 99.5 % (Table 4). There was no effect of intra- or inter-specific densities on *Mercenaria mercenaria* survival. In the lower food trial, survival rates were reduced, ranging from 65 to 88 % (Table 4). There were significant ($p < 0.05$) intra- and inter-specific density effects on survival of newly settled hard clams, although the differences were relatively small. Multiple comparisons among means (Welsch step-up procedure) showed no significant negative intra- or inter-specific density effect on survival.

In Growth Expt 2, effect of gem clams on post-settlement *Mercenaria mercenaria* growth was strikingly different in sand and muddy sand. In sand, dense *Gemma gemma* populations consistently enhanced hard clam growth, as they did in Growth Expt 1. In muddy sand, the same *G. gemma* density reduced hard clam growth (Fig. 4). The effects of *G. gemma*, Sediment, and *G. gemma* × Sediment interaction all were significant (Table 5). Interestingly, the fastest growth rate occurred in muddy sand without *G. gemma*.

Survival rates were > 90 % among treatments except in muddy sand containing gem clams (Table 6). *Gemma gemma*, Sediment and *G. gemma* × Sediment interaction significantly affected *Mercenaria mercenaria* survival (Table 7). Thus both survival and growth of hard clams were reduced in the presence of gem clams in muddy sand.

### Mechanisms of growth enhancement

In Mechanism Expt 1 hard clams grew faster in shallower sediments in both trials (Fig. 5). Trends were similar in both trials while pairwise comparisons differed slightly (Fig. 5).

Table 5. Growth Expt 2. Two-way ANOVA table for the effects of *Gemma gemma* density and sediment type on *Mercenaria mercenaria* growth. •••$p < 0.001$; ••$0.001 < p < 0.01$

| Source | SS | df | MS | $F_S$ | |
|---|---|---|---|---|---|
| *G. gemma* | 24 112 | 1 | 24 112 | 8.64 | •• |
| Sediment | 44 352 | 1 | 44 352 | 15.89 | ••• |
| *G. gemma* × Sediment | 186 832 | 1 | 186 832 | 66.95 | ••• |
| Error | 1 328 393 | 476 | 2 791 | | |

Table 6. Growth Expt 2. Effect of *Gemma gemma* and sediment type on *Mercenaria mercenaria* survival. Survival rate expressed as percentage of clams remaining alive at the end of the experiment to the total number retrieved. Means (SD) for 3 replicate samples. Initial mean shell length of hard clams was 226 µm in both sediment types. Mean shell length of *G. gemma* was 2.9 mm. •••Survival rate of hard clams was significantly ($p < 0.001$) reduced in presence of gem clams in muddy sand; interaction term between *G. gemma* and sediment (2-way ANOVA; $F_S$ = 13.1968) is highly significant ($p < 0.01$)

| Sediment type | *G. gemma* 10 cm$^{-2}$ | |
|---|---|---|
| | 0 | 120 |
| Sand | 97.2 (1.14) | 92.0 (4.38) |
| Muddy sand | 98.6 (1.61) | 81.6 (2.84)••• |

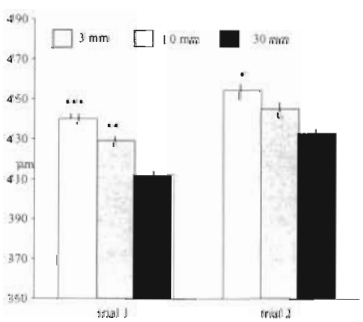


Fig. 5. Mechanism Expt 1. Effect of sediment thickness on growth of newly settled *Mercenaria mercenaria*. Means (±1 SE) of final shell length (µm) for 3 replicate samples (33 subsamples for each replicate in Trial 1, 40 in Trial 2). Mean initial shell length of *M. mercenaria* was 215 µm in Trial 1, 226 µm in Trial 2. •$0.01 < p < 0.05$; ••$0.001 < p < 0.01$; •••$p < 0.001$

Table 7 Growth Expt 2. Two-way ANOVA table for the effects of *Gemma gemma* density and sediment type on *Mercenaria mercenaria* survival. •••$p < 0.001$; ••$0.001 < p < 0.01$; •$0.01 < p < 0.05$

| Source | SS | df | MS | $F_S$ | |
|---|---|---|---|---|---|
| *G. gemma* | 383.6 | 1 | 386.6 | 47.4 | ••• |
| Sediment | 60.6 | 1 | 60.6 | 7.8 | • |
| *G. gemma* × Sediment | 102.6 | 1 | 102.6 | 13.2 | •• |
| Error | 62.2 | 8 | 7.8 | | |

Mechanism Expt 2 showed that $^{14}C$ retention efficiency of radiolabeled biodeposits by newly settled *Mercenaria mercenaria* averaged only 4.5 % (± 0.56 SE), much lower than the 76.7 % (± 0.78) absorption of $^{14}C$-*Isochrysis galbana*.

In Mechanism Expt 3, hard clams exposed to high input of *Gemma gemma* biodeposits grew more slowly than control clams (Fig. 6). Addition of a small amount of biodeposits had no effect on growth.

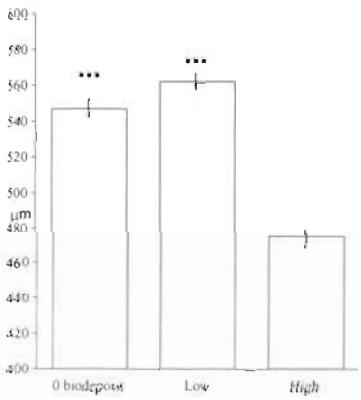


Fig. 6. Mechanism Expt 3. Effect of *Gemma gemma* biodeposit addition on *Mercenaria mercenaria* growth. Means (± 1 SE) of final shell lengths (µm) for 3 replicate samples (n = 120; 40 from each replicate). Initial size of *M. mercenaria* was 257 µm. Low biodeposit was collected from ca 25 *G. gemma* (3 mm in shell length); high biodeposit was collected from ca 100 *G. gemma*. •••Significantly ($p < 0.001$) different from high treatment. There was no significant difference between control and low addition treatment

## DISCUSSION

We were surprised to find that dense assemblages of *Gemma gemma* could enhance growth of *Mercenaria mercenaria* post-settlement. There are no theories or studies that would have led to predict these results. Most studies have shown negative effects of dense assemblages on growth (Williams 1979, Peterson & Andre 1980, Peterson 1982, Peterson & Black 1987, Gallagher et al. 1990), settlement (Sanders et al. 1962, Woodin 1976, Williams 1980, Peterson 1982) and emigration (Muus 1973, Luckenbach 1984), but Wilson (1981) made a critical point that relative and absolute sizes of interacting species may play 'a crucial role in determining the outcome of interspecific or inter-functional group interactions'. This is especially the case for interference, and less so for exploitative competition.

Emigration experiments demonstrated that hard clams in dense patches of gem clams

quickly moved away. Microscopic observation showed that emigration from the cylinders occurred within a few days after transplantation. Once they emigrated from the crowded cylinders, they ceased crawling and anchored themselves to sand grains using byssal threads. Most emigrants were found near borders between cylinders and surrounding plots. Hard clams remaining in cylinders containing gem clams were scattered, and alternated between crawling, burrowing and byssal attachment. It is possible that hard clams accidentally fell from cylinders due to reworking by gem clams. The fact that the effect of gem clams on hard clam emigration was enhanced at the lower food concentration implies that emigration was not totally accidental.

Emigration rates were higher in the field experiment (Emigration Expt 2) than in the laboratory; emigration rates were as high as 41.3 % over a 3 d period in the presence of *Gemma gemma* and 23.7 % in its absence (Fig. 2). Cage baffling caused accumulation of a 2 mm layer of mud in containers left for 3 d in the field site (e.g. Nowell & Jumars 1984). Deposition may have made the substrate less favorable for newly settled hard clams, and could have caused them to migrate out of the cages.

Newly settled hard clams may have moved away from *Gemma gemma* because the larger gem clams destabilized the sediment, making it locally unsuitable for small postlarvae (Rhoads & Young 1970, Luckenbach 1984, Posey 1990). Interference of feeding by resuspension was probably more important in muddy sand than in sand, but the difference in emigration rates between sand and muddy sand was not as great as the difference between presence and absence of gem clams. An alternative mechanism is interference by direct contact. Significant emigration under lower algal concentration with gem clams indicates that emigration might also have been driven partly by exploitative competition for food.

The most surprising results of this study demonstrated that *Gemma gemma* could enhance post-settlement growth of hard clams, but their influence was altered greatly by sediment type (Fig. 4). In sand, increased *G. gemma* density consistently enhanced *Mercenaria mercenaria* growth (Fig. 3). During these experiments, brooding gem clams released as many as 2000 juveniles $well^{-1}$ (at the high adult density), especially under high food concentration. Juvenile gem clams were similar in size (300 to 400 µm) and behavior to post-settlement *M. mercenaria*. Nevertheless, hard clams grew better in sand when crowded with adult and juvenile *G. gemma* than in their absence. In muddy sands the reverse was true (Fig. 4); juvenile hard clams grew much better in the absence of *G. gemma*. Curiously, growth in muddy sands without *G. gemma* exceeded that in sands with *G. gemma* (Fig. 4). Unbioturbated muddy sand can be compacted and not easily penetrable, a condition which may be conducive to growth of suspension feeders (Rhoads & Young 1970).

The effect of the *Gemma gemma*-sediment type interaction on *Mercenaria mercenaria* growth could be explained by a single mechanism; any factor that keeps small hard clams at the sediment surface results in greater growth. Enhanced growth in shallower sediment (Fig. 5) supports the suggestion that longer surface residence time increases *M. mercenaria* growth, perhaps due to increased feeding time. Post-settlement *M. mercenaria* do not have siphons, so it is likely that they feed only when at or very near the sediment surface (Carriker 1961). There is no evidence that they deposit-feed.

This mechanism provides a reasonable explanation for *Mercenaria mercenaria* growth in muddy sand. In the absence of bioturbating gem clams, muddy sand would be somewhat compacted and have a thin oxidized layer overlying a reduced layer, both of which would keep hard clams near the sediment surface. Bioturbation by gem clams makes muddy sand a much poorer substrate for post-settlement *M. mercenaria*; it increases the water content, making sediment less stable for small suspension feeders and increases the likelihood of being clogged with fine sediment (Rhoads & Young 1970). Elmgren et al. (1986) demonstrated the converse for a deposit-feeding bivalve; in the presence of amphipods, spat survived less in a shallow sediment than in a thicker layer.

We suggest that the same mechanism, increased surface residence, can explain enhanced growth of newly settled hard clams in the presence of *Gemma gemma* in clean sand. Microscopic observations indicated that when newly settled hard clams crawl (e.g. when they emigrate from gem clam patches), they stay at or within a few grain layers from the sediment surface. Thus, hard clams may spend more time at the surface when they emigrate from *G. gemma* patches. We suggest further that they suspension-feed while they crawl, so they spend more time eating when they are migrating than when they stay put. This scenario is speculative and would be totally unconvincing except that it is consistent with enhanced *Mercenaria mercenaria* growth in a thin layer of sediment (Fig. 5). It is possible that growth was enhanced because there was more effective pore water exchange in the thin sediment layer, but the fact that very clean sand was used in this experiment lessens the likelihood that metabolite buildup in the pore water affected hard clam growth. It is more likely that clams in a thin layer of sediment were continuously exposed to overlying suspended algae, while those in deeper layers partitioned

their time between surface feeding and deeper burrowing. Further investigation is needed to test this suggested interpretation, but it is consistent with all of our data.

There is an intriguing implication of this suggested interpretation regarding selective pressures on early life history of *Mercenaria mercenaria*, and perhaps many other burrowing, suspension-feeding bivalves. Undisturbed hard clams in sand grow more slowly than those constrained to the sediment surface. They appear not to grow at maximum rate unless they are kept at the surface, despite the obvious advantages to growing out of this vulnerable size class. Epibenthic predation is the probable selective pressure counteracting surface suspension-feeding (Muus 1973, Peterson 1979). Clams partition time between the necessary risk of surface suspension-feeding and the safe but energetically unprofitable deeper refuge. Interaction between opposing selective pressures is often invoked but is rarely taken into account in interspecific competitive interactions.

Growth enhancement in sand was not due to utilization of *Gemma gemma* feces and pseudofeces by *Mercenaria mercenaria*. Low retention efficiencies of *G. gemma* biodeposits by *M. mercenaria* indicate that biodeposits were ingested but were only slightly absorbed. Microscopic examination showed that *G. gemma* biodeposits produced from 5 to 6 $\times$ $10^5$ cells $ml^{-1}$ algal food consisted mostly of feces. Hence, that biodeposits had little nutritional value for newly settled hard clams is reasonable. The 'particle' size of biodeposits ( 20 to 30 µm diameter compared to 4 µm for *Isochrysis galbana*) may have reduced ingestion rates.

Growth reduction at high concentration of biodeposits indicates that biodeposition by a dense gem clam population did not contribute to enhanced hard clam growth. At high deposition rates, biodeposits might reduce hard clam growth by clogging gills or by stimulating metabolite buildup. Addition of low concentrations did not reduce growth of newly settled hard clams. Biodeposition could be beneficial to some deposit feeders (Commito & Boncavage 1989), but not for newly settled, suspension-feeding hard clams.

Survival rates of *Mercenaria mercenaria* were very high and were not affected by intra- or inter-specific densities at high food concentration (Table 4). Survival rates were reduced at lower food levels. Difference in survival rates may have resulted from using different batches of clams and food rather than from food concentration. Overall, dense *Gemma gemma* populations did not reduce survival of newly settled hard clams in sand even when food was restricted.

Dense *Gemma gemma* populations in muddy sand did reduce hard clam survival (Table 6). Microscopic examination showed that dead hard clams were close to their initial size, indicating either that death occurred early in the experiment, or that clams with lower growth rates did not survive. Burial by sediment reworking, together with exposure to pore water metabolites, may have contributed to mortality. However, even at the highest *G. gemma* density in muddy sand, hard clams survival was > 80 %. Dense patches of gem clams do not appear to severely affect survival of newly settled hard clams.

*Gemma gemma* density and sediment grade had complex effects on patterns of growth and emigration of early post-settlement *Mercenaria mercenaria*, which can be interpreted by postulating that any mechanism that increases surface residence time leads to more rapid growth of hard clams. This mechanism could explain why hard clams grew faster in a shallow layer of sand than in a deeper layer of the same clean sediment. We suggest that enhanced growth in sand in presence of *G. gemma* was an indirect effect of increasing emigration rate; clams may migrate mostly at the sediment surface. Results in muddy sand are also consistent with the proposed mechanism. The primary implication of this explanation is that early post-settlement, asiphonate hard clams do not grow as fast as they could at a given food concentration because the opposing selective pressures require hard clams to partition time between necessary surface feeding and deeper refuge from surface predation.

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