Effects of suspended food availability on the feeding mode and burial depth of the Baltic clam, Macoma balthica

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Lin, J and Hines, A. H. 1994. Effects of suspended food availability on the feeding mode and burial depth of the Baltic clam, Macoma balthica. – Oikos 69: 28–36.

Previous studies showed that siphon cropping by epibenthic predators reduces the size of inhalant siphon of the Baltic clam Macoma balthica (L.), causing the clams to reside at shallower burial depths in the sediment and making them more vulnerable to lethal predation. This indirect interaction is further complicated because M. balthica facultatively switches between suspension- and deposit-feeding in response to the availability of suspended food particles. Laboratory experiments showed that the proportion of clams deposit feeding with exposed siphons increased with decreasing food concentrations in the water column and this resulted in shallower burial depths in the sediment. The clams showed similar responses in feeding mode and burial depth to the concentrations of suspended food indirectly manipulated by the presence and/or density of either interspecific (suspension-feeding soft-shelled clam Mya arenaria L.) or intraspecific competitors.

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Higher-order interactions and indirect effects involving multiple trophic levels and environmental factors are widespread in marine (e.g., Dungan 1986, Schmitt 1987, Kneib 1988, Peterson and Black 1988, Wilson 1989, Posey and Hines 1991), freshwater (e.g., Morin 1986, Miller and Kerfoot 1987, Sih 1987, Sadinski and Dunson 1992, Werner 1992), and terrestrial communities (e.g., Miller 1985, Wilson 1986). An understanding of these complex multispecies interactions is essential to synthetic theories of population and community structure. The complexity of the interactions, however, often makes it difficult to detect higher-order interactions and/or distinguish direct and indirect effects (Connell 1983).

The Baltic clam Macoma balthica (L.) offers an ideal model system to examine the role of indirect effects and complex interactions on trophic interactions. It is a facultative suspension and deposit feeder. Bubnova (1972) and 'Olafsson (1986) hypothesized that M. balthica suspen-

sion feeds when suspended food particles are abundant and deposit feeds when the suspended food supply decreases. Recent studies (Hummel 1985, Thompson and Nichols 1988, Beukema and Cadée 1991) found that the greater part of food for M. balthica originates from the water column, despite the fact that the clam's functional morphology is better equipped for deposit feeding (Gilbert 1977). The clam is able to filter food from the overlying water while the inhalant siphon is just at the surface of the substrate (Brafield and Newell 1961, Hummel 1985). While deposit feeding, however, the clam extends its inhalant siphon over the sediment surface (Zwarts and Wanink 1989). This may require a reduction of the clam's burial depth, making it vulnerable to predation by blue crabs, birds, and other epibenthic predators (Reading and McGrorty 1978, Blundon and Kennedy 1982), as well as increasing its accessibility to siphon cropping by fishes (de Vlas 1979, 1985, Hines et al.
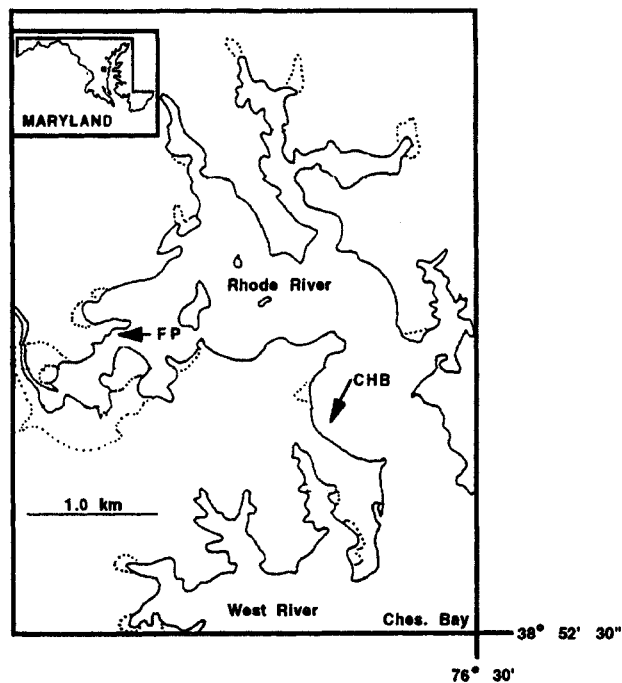
Fig. 1. Map of Rhode River showing location of sampling sites: Fox Point (FP) and Canning House Bay (CHB). Ches. Bay = Chesapeake Bay.

1990). Siphon cropping may further reduce the clam's burial depth and make it even more susceptible to lethal predation (de Vlas 1985). By shifting from deposit to suspension feeding, *M. balthica* might be able to increase its burial depth (Zwarts and Wanink 1989) and thus minimize sub-lethal and lethal predation.

The present study describes a series of laboratory experiments in which we either directly or indirectly (through inter- or intra-specific competition) manipulated the availability of suspended food to *M. balthica*. The objective was to test the hypothesis that reduced food concentration in the water column resulted in more clams adopting deposit feeding and consequently having a shallower burial depth in the sediment.

Materials and methods

Field sampling

To estimate density and size frequency distribution of *M. balthica* in the field, two sampling sites (Fox Point and Canning House Bay) were established in the Rhode River subestuary, located in the lower mesohaline zone of the western shore of the Chesapeake Bay, USA (Fig. 1). Both sites were subtidal with a water depth of 1.5 to 2 m. The sediment composition was about 10% sand (≥ 63 μm) and 90% mud (< 63 μm) at both sites. Cylindrical core samples (80 cm^2 surface area and 60 cm deep) from the two sites were collected at approximately monthly intervals

between 27 April and 27 July of 1990. Seven to eight samples (each sample consisted of five haphazardly located cores) were taken at each site during each monthly sampling. The sediment from the five cores was sieved through a 1-cm mesh screen except on 25 June and 24 July at Fox Point when a 2-mm mesh screen was used. All *M. balthica* found were counted and all or subsamples of the clams were measured (shell length to the nearest 0.1 mm).

To examine the vertical distribution of *M. balthica*, intact cores were extruded immediately upon extraction into a horizontal PVC trough, and quickly and carefully cut into 2-cm sections. Burial depth (average distance from sediment-water interface to the beginning and end of the 2-cm section) and shell length of nine to 11 clams were measured and recorded at each site during each monthly sampling.

Burial depth in a bivalve might be determined by the length of inhalant siphon which the animals uses to collect food and oxygen from the surface and overlying water (Ansell 1962, Trueman et al. 1966). Siphon length, however, was difficult to measure because the siphon is elastic (Zwarts and Wanink 1989). Siphon weight was measured instead. During May, June, and July monthly samplings, the clams whose burial depths were measured were brought back to the laboratory where they were dissected. The inhalant siphon of each clam was removed (Zwarts and Wanink 1989) and dried to a constant weight at 60°C.

Laboratory experiments

All the *M. balthica* used in the experiments were collected from Fox Point and ranged in shell length from 29 to 36 mm, sizes commonly found in the field. The experiments were conducted at the Smithsonian Environmental Research Center. Estuarine water used in the experiment was pumped from the Rhode River near the collection site.

Effects of food availability in the water column
The first experiment was to manipulate directly the food availability in the water column to test its effect on *M. balthica*'s feeding mode and burial depth. Three clams were haphazardly assigned to each 3.5-liter glass jar (about 154 m^2 and 23 cm deep) containing 20 cm depth of sand [coarse sand (> 500 μm): 16%, medium sand (250–500 μm): 56%, fine sand (125–250 μm): 28%] and 400 ml of water. The clam density used in the experiment was slightly above average densities found in the field. A known length nylon thread with a numbered tag was attached to each clam with adhesive. By measuring the length of the thread remaining above the sediment surface, the depths to which the clams were subsequently buried (depth from substrate surface to top of the shell) could be determined (Zwarts 1986).

The jars were divided into three groups fed with, re-

spectively: 1. estuarine water with addition of cultured microalgae; 2. natural estuarine water; and 3. filtered estuarine water. The water was changed twice daily (at about 0900 and 1600 hours, respectively). For group 1, 100 ml of pure cultured alga (*Isochrysis* sp.) was mixed with 300 ml fresh estuarine water and added to each jar during each water change. For group 3, the estuarine water was filtered through a 1 µm mesh bag before being supplied to the jars. An air stone was put in each jar to provide circulation. A completely randomized design was used with eight replicate jars for each of the three groups.

The experiment was conducted during September, 1989. Water temperature in the jars ranged from 21°C to 25°C. On September 8, water samples were taken from each jar to measure their chlorophyll a concentrations spectrophotometrically (Parsons et al. 1984).

Feeding activities of the clams were observed for about ten minutes for ten times at haphazard intervals during the experiment. Number of clams exhibiting deposit feeding (the inhalant siphon makes whirling and scraping movements over the sediment surface and sucks in the uppermost layers of the sediment – Hulscher 1982) or suspension feeding (the inhalant siphon was held straight up and relatively still in the water column – 'Olafsson 1986) in each jar was recorded. Burial depth of each clam was determined every two to three days until the clams' burial depth became stable.

Effects of interspecific competition
Different densities of the suspension-feeding soft-shelled clam (*Mya arenaria* L.) were confined to plastic buckets (0.05 m² – surface area and 35 cm deep) with *M. balthica* (four per bucket) to examine the effects of interspecific competition for suspended food on *M. balthica*'s feeding mode and burial depth. The density of *M. balthica* used in the experiment represented the lower range of natural densities found in the field. There were three density treatments of *M. arenaria*: zero, three (low density), and six (high density) clams per bucket. These represent the range of natural *M. arenaria* densities in Rhode River (Hines and Comtois 1985, Hines et al. 1990). There were two small (40–50 mm in shell length) and one large (60–70 mm in shell length) *M. arenaria* in each bucket for the low density treatment, and four small and two large *M. arenaria* in each bucket for the high density treatment. *M. arenaria* were collected from the Chesapeake Bay and/or purchased from a local seafood market. Each bucket was filled with sandy mud sediment from the Canning House Bay [medium sand: 25%, fine sand: 40%, very fine sand (63–125 µm): 21%, mud (<63 µm): 14%] to a depth of 23 cm and six liters of natural estuarine water. The water was changed twice daily (at about 0900 and 1600 hours, respectively). An air stone was put in each bucket to provide circulation. A completely randomized design was used with five replicate buckets for each group.

The experiment was conducted in October and November of 1989. Water temperature in the buckets ranged from 14°C to 19°C. A water sample was taken from each bucket to determine chlorophyll a concentration spectrophotometrically (Parsons et al. 1984). Water samples were taken on 19 October, three hours after the morning water change; on 25 October, seven hours after the morning water change; and on 26 October, 17 hours after the previous water change on the afternoon of 25 October. Feeding activities of the clams were observed for about ten minutes at irregular intervals for 22 times during the experiment. The number of *M. balthica* exhibiting deposit or suspension feeding behavior was recorded. Burial depths of *M. balthica* were measured every three to four days until the clams' burial depth became stable.

Effects of intraspecific competition
Three densities of *M. balthica* (low, medium, and high with five, ten, and 20 clams per bucket, respectively) with six replicates for each density treatment were confined in buckets (0.05 m² – surface area and 35 cm deep) to examine the effects of density on the clam's feeding mode and burial depth. Each bucket was filled with 23 cm depth of sediment from Canning House Bay (medium sand: 20%, fine sand: 49%, very fine sand: 21%, and mud: 10%) and six liters of natural estuarine water. The clam densities used in the experiment represent lower, medium, and higher ranges of natural *M. balthica* densities found in the field. The water was changed twice daily (at about 0900 and 1600 hours, respectively) and one airstone was provided for each bucket. The experiment was conducted in November and December of 1989. Water temperature in the buckets during the experiment ranged between 9°C and 15.5°C.

Water samples were collected from each bucket for suspended particle concentration measurements (number of particles/0.5 ml) with a model A Coulter Counter (aperture size: 100 µm). During the experiment, water samples were taken four times just before the morning and afternoon water changes, respectively. To examine the relationship between concentrations of suspended particles and chlorophyll a, water samples with different particle concentrations were measured both with the Coulter Counter (for particle concentration) and with the spectrophotometer (for chlorophyll a).

Feeding activities of the clams were observed for about ten minutes at irregular intervals on six occasions during the experiment. The numbers of clams exhibiting deposit and suspension feeding behavior were recorded. In addition, for deposit feeding clams, we also recorded whether the clam's inhalant siphon extended more or less than 1 cm from the siphon hole. Burial depths of the clams were measured every seven days until the clams' burial depth became stable.
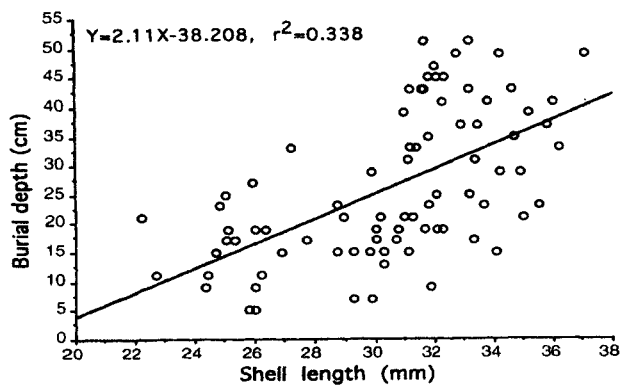
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Fig. 2. Regression between shell length and burial depth for *M. balthica*. The data were pooled over the two sampling sites (Fox Point and Canning House Bay) and the four monthly samplings (April, May, June, and July).
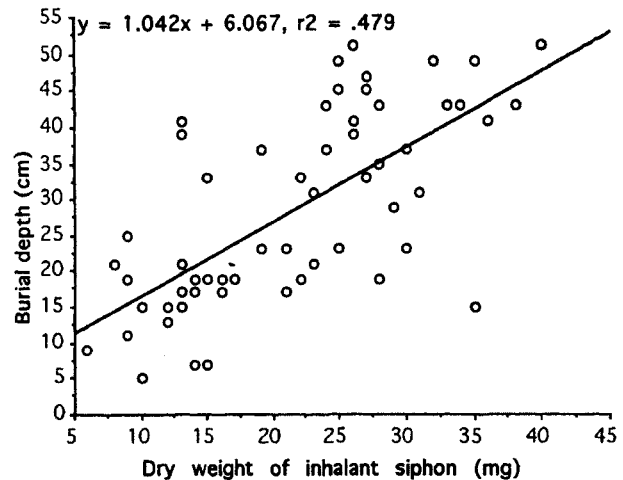

Fig. 3. Regression between inhalant siphon dry weight and burial depth for *M. balthica*. The data were pooled over the two sampling sites (Fox Point and Canning House Bay) and the three monthly samplings (May, June, and July).

Results

Field sampling

There was a significant effect of sampling site ($F_{1,55}$ = 11.12, P = 0.002) on density of *M. balthica* whereas the effects of month ($F_{3,55}$ = 0.07, P = 0.98) and site × month interaction ($F_{3,55}$ = 0.84, P = 0.48) were not significant as analyzed by a two-way analysis of variance (ANOVA). Mean (s.e., n) densities of clams were 8.1 (0.5, 31) and 6.0 (0.4, 32) per sample (one sample consisted of five cores) at Fox Point and Canning House Bay, respectively. Similarly, sampling site had a significant effect ($F_{1,326}$ = 64.48, P = 0.0001) on shell length whereas the effects of month ($F_{3,326}$ = 1.22, P = 0.30) and site × month interaction ($F_{3,326}$ = 1.01, P = 0.39) were not significant as analyzed by a two-way ANOVA. Mean (s.e., n) shell lengths of *M. balthica* were 32.6 (0.2, 174) and 29.4 (0.3, 160) mm at Fox Point and Canning House Bay, respectively.

Burial depth of the clams increased with increasing shell length when the data were pooled over the two sites and four monthly samples ($F_{1,80}$ = 40.33, P = 0.0001, r^2 = 0.34, Fig. 2). Burial depth of the clams also increased with increasing dry weight of inhalant siphon when the data were pooled over the two sites and the May, June, and July monthly samples ($F_{1,59}$ = 53.43, P = 0.0001, r^2 = 0.48, Fig. 3).

Laboratory experiments

Effects of food availability in the water column
Average (s.e.) chlorophyll a concentrations were 75.1 (11.0), 15.5 (1.3), and 8.3 (1.5) µg l⁻¹ for the groups fed with supplemental algae, natural water, and filtered water, respectively. There was a significant effect of treatment on chlorophyll a concentration as analyzed by a one-way ANOVA ($F_{2,20}$ = 30.43, P < 0.0001). Chlorophyll a concentration was significantly higher for the group fed with algae than for the other two groups, whereas the

difference between the other two groups was not significant (Tukey's multiple comparison test at 0.05 level).

On average, 18.3% (s.e. = 2.8%, n = 10) of the clams were feeding during each observation. There was a significant effect of the treatment on the proportion of feeding clams that adopted suspension feeding ($F_{2,29}$ = 3.71, P = 0.04, one-way ANOVA). Average proportion of the clams that adopted suspension feeding was significantly higher for the group fed with algae (0.92, s.e. = 0.05, n = 10) than the groups fed with natural water (0.59, s.e. = 0.12, n = 10) and with filtered water (0.60, s.e. = 0.11, n = 10), whereas there was no significant difference between the latter two groups (Tukey's multiple comparison test at 0.05 level).

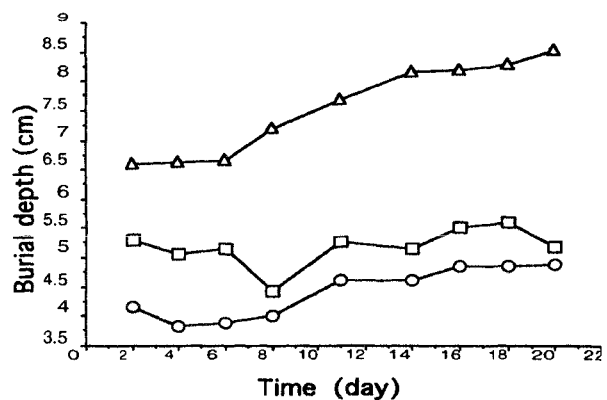The clams began to show differences in mean burial

Fig. 4. Average burial depths of *M. balthica* over time for the groups supplied with cultured algae (triangles), natural (squares) and filtered (with 1 µm mesh bag) estuarine water (circles). Error bars are not shown to avoid overcrowding the figure. The standard errors of the average final burial depths (on the 20th day) were 1.4, 0.8 and 0.8 cm for the groups fed with algae, natural and filtered water, respectively.

Table 1. Mean (s.e.) concentration of chlorophyll a ($\mu g\ l^{-1}$) in the water for the three groups of *M. balthica* confined with different densities of *M. arenaria*. Water samples were taken three, seven, and 17 h after the previous water change on October 19, 25 and 26 October, respectively. Means connected by underline are not significantly different from each other (Tukey's multiple comparison test at 0.05 level).

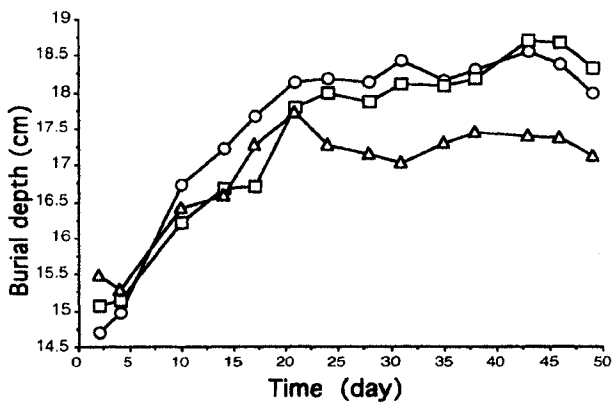| Date	Zero *M. arenaria*	Low density of *M. arenaria*	High density of *M. arenaria*
19 October	8.8 (2.3)	4.7 (1.2)	1.3 (0.5)
25 October	7.3 (0.5)	0.4 (0.1)	0.1 (0.1)
26 October	3.4 (0.9)	0.9 (0.2)	1.3 (0.4)

Fig. 5. Average burial depths of *M. balthica* over time for the groups with zero (circles), low density (squares), and high density *M. arenaria* (triangles). Four *M. balthica* were confined with zero, three, or six *M. arenaria* per bucket, respectively for the three groups. Error bars are not shown to avoid overcrowding the figure. The standard errors of the average final burial depths (on the 47th day) were 1.2, 1.1 and 1.1 cm for the groups with zero, low and high density *M. arenaria*, respectively.

depth among the treatments after only two days from the initiation of the experiment when the first depth measurements were taken (Fig. 4). Whereas the clams fed with supplemental algae continued to bury themselves deeper, the clams of the other two groups maintained relatively constant burial depth throughout the experiment (Fig. 4). One-way ANOVA revealed a significant difference ($F_{2,21} = 3.76$, $P = 0.04$) in the final mean burial depth among the three groups of clams. Tukey's multiple comparison test (at 0.05 level) showed that the final mean burial depths of clams for the group fed with algae was significantly higher than those of the other two groups, whereas there was no significant difference between the other two groups.

Effects of interspecific competition

Separate one-way ANOVAs showed a significant effect of treatment (P < 0.05) on mean chlorophyll a concentrations in the water ($\mu g\ l^{-1}$) for the 19, 25 and 26 October samples. In general, chlorophyll a concentration was significantly higher for the group with zero *M. arenaria* than those with low and high densities of *M. arenaria*, whereas the chlorophyll a concentration did not differ significantly between the latter two groups (Table 1).

On average, 42.9% (s.e. = 2.2%, n = 22) of the *M. balthica* were feeding during each observation. There was a significant effect of the treatment on the proportion of feeding clams that adopted suspension feeding ($F_{2,65} = 5.89$, $P = 0.005$, one-way ANOVA). Average proportion of the clams that adopted suspension feeding was significantly higher for the group with zero *M. arenaria* (0.77, s.e. = 0.05, n = 22) than the groups with low (0.60, s.e. = 0.05, n = 22) and high densities of *M. arenaria* (0.54, s.e. = 0.05, n = 22), whereas there was no significant difference between the latter two groups (Tukey's multiple comparison test at 0.05 level).

Burial depths of *M. balthica* were similar among the treatments until 22 d into the experiment when the group with high density *M. arenaria* seemed to diverge from the other two groups (Fig. 5). However, due to large variations among the replicates, the difference among the treatments in final burial depth was not significant ($F_{2,12} = 0.37$, $P = 0.70$, one-way ANOVA).

Effects of intraspecific competition

Separate two-way ANOVAs were used to test the effects of experimental treatment and date on the suspended particle concentrations before morning and afternoon water changes. For the samples taken before morning water change, both treatment ($F_{2,60} = 3.49$, $P = 0.04$) and date ($F_{3,60} = 9.30$, $P = 0.0001$) had significant effects, whereas their interaction did not ($F_{6,60} = 0.83$, $P = 0.55$). When the data were pooled over the dates, the effect of treatment is marginally significant ($F_{2,71} = 2.59$, $P = 0.08$, one-way ANOVA). Mean (s.e., n) particle concentrations for the low, medium, and high density *M. balthica* were 431 (46, 24), 334 (35, 24), and 312 (36, 24), respectively.

Effects of treatment ($F_{2,59} = 11.87$, $P = 0.0001$), date ($F_{3,59} = 21.90$, $P = 0.0001$), and their interaction ($F_{6,59} = 2.65$, $P = 0.024$) were all significant for the afternoon samples. Separate ANOVAs showed that the treatment

Table 2. Mean concentration of suspended particles (s.e.) (number/0.5 ml) just before the afternoon water change for the groups of low (five per bucket), medium (ten per bucket), and high density clams (20 per bucket). Water samples were taken from each of the six replicate buckets for each group. P values of one-way ANOVA is shown for each sample. If ANOVA result was significant (at 0.05 level), a Tukey's multiple comparison's test was performed and means not significantly different at 0.05 level are connected by underline.

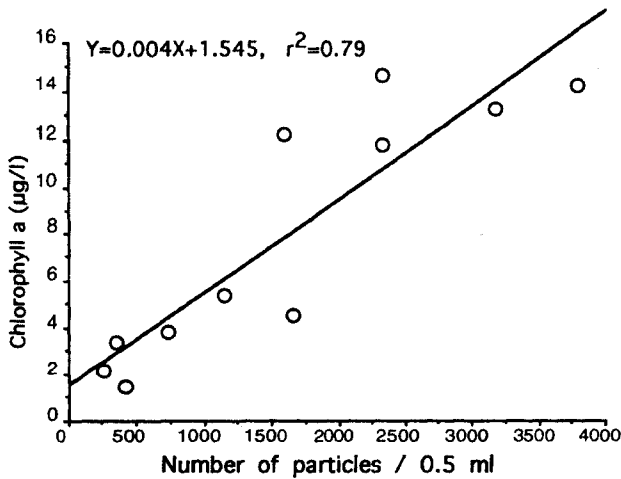| Date (M/D)	Low Density	Medium Density	High Density	P (ANOVA)
12/7	1643 (163)	1297 (307)	1269 (190)	0.460
12/11	5568 (638)	3141 (500)	2591 (847)	0.016
12/12	3976 (886	1266 (241)	1500 (648)	0.018
12/13	781 (144)	1066 (533)	569 (161)	0.443

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$Y=0.004X+1.545, \ r^2=0.79$

Fig. 6. Regression between concentrations of chlorophyll a and suspended particles (<100 µm) in the water samples.

effect was significant in two out of the four dates (Table 2). In both dates, the particle concentration was higher for the low density group than for the medium and high density groups, whereas there was no significant difference between the latter two groups (Tukey's multiple comparisons test at 0.05 level, Table 2).

There was a strong ($r^2 = 0.79$) and positive linear relationship (P = 0.0003) between concentrations of chlorophyll a and suspended particles (Fig. 6).

On average, 40% (s.e. = 6%, n = 6) of the clams were feeding during each observation. The effect of the treatment on the proportion of feeding clams that adopted suspension feeding was not significant ($F_{2,17} = 0.86$, P = 0.44, one-way ANOVA). Average (s.e.) proportion of the clams that adopted suspension feeding over the six observations was 0.71 (0.05), 0.64 (0.06), and 0.70 (0.04) for the low, medium, and high density treatments, respectively. For the clams observed deposit feeding, the effect of treatment on the proportion with inhalant siphon protruding more than 1 cm from the siphon hole was also not significant ($F_{2,15} = 0.86$, P = 0.44, one-way ANOVA). Average proportion (s.e.) of the clams with extended siphon was 0.40 (0.19), 0.65 (0.10), 0.60 (0.12) for the groups of low, medium, and high density of clams, respectively.

Density had a significant effect ($F_{2,15} = 4.72$, P = 0.03, one-way ANOVA) on the final mean burial depth of *M. balthica*. Tukey's multiple comparisons test (at 0.05 level) revealed that clams of high density buried at a shallower depth than those of medium and low densities, whereas the burial depths were similar between the latter two groups (Fig. 7).

Discussion

Burial depth of *M. balthica* increased with both increasing shell length and dry weight of the inhalant siphon, although with large variations (Figs 2 and 3). These results correspond with previous findings for *M. balthica* populations on the east coast of England (Reading and McGrorty 1978), the Dutch Wadden Sea (Zwarts and Wanink 1989; P. Kamermans, pers. comm.), in North Carolina (P. Kamermans, pers. comm.) and at other locations in Chesapeake Bay (Blundon and Kennedy 1982, Hines and Comtois 1985). The siphon weight is a slightly better predictor of burial depth than the shell length for the clams as indicated by higher r^2 (Figs 2 and 3). In addition to siphon length, burial depth of a clam may also be determined by its feeding mode. Because suspension feeders only need to reach the surface, while deposit feeders have to use part of the siphon to graze on the surface, it might be expected that burial depth in deposit-feeding individuals is more variable than that in suspension-feeding ones.

Our three experiments all suggest that the clams were mainly suspension feeders when food was abundant in the water column, but switched to deposit-feeding when the suspended food concentrations were low. Increased proportions of clams adopting deposit-feeding may have resulted in the shallower burial depths, as suggested by Zwarts and Wanink (1989). The initial and final shell lengths of all individual clams were virtually identical in all the three experiments. In addition, the divergence in burial depths began early (in several days in the food availability and intraspecific competition experiments and in 20 d in the interspecific competition experiment)
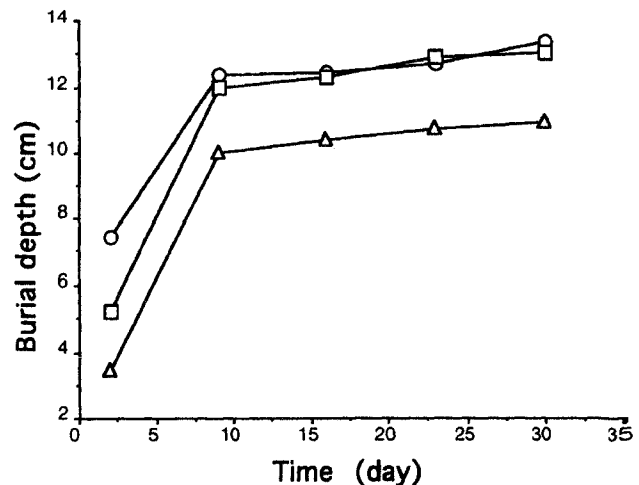

Fig. 7. Average burial depths of *M. balthica* over time for the groups of low (circles), medium (squares), and high density (triangles). There were five, ten, and 20 clams per bucket for the low, medium, and high density groups, respectively. Error bars are not shown to avoid overcrowding the figure. The standard errors of the average final burial depths (on the 30th day) were 0.6, 0.5 and 0.7 cm for the groups of low, medium, and high density, respectively.

in all three experiments. Therefore the differences in burial depth among the treatments observed were not likely due to differential growth rates of clams resulting from different levels of food supply during the experiments.

Burying deep in the sediment is one of the few defensive mechanisms against epibenthic predators for a thin shelled bivalve like *M. balthica* (e.g., Blundon and Kennedy 1982, Commito 1982, Zwarts and Wanink 1984, Haddon et al. 1987). Suspension feeding may also reduce the risk of the siphon being cropped by epibenthic predators. Many species of fish and shrimps crop siphons of *M. balthica* as food (de Vlas 1979, 1985, Hines et al. 1990). Siphons of *Macoma* were major food items for two of the four dominant epibenthic predators in Rhode River (Hines et al. 1990). Individual clams may have lost an average of several siphon tips per day and siphon tissue loss amounted to nearly half of the annual mean biomass of the soft parts for a *M. balthica* population from the Dutch Wadden Sea (de Vlas 1985). Loss of the siphon may force the clams to reside at a shallower depth and make them even more vulnerable to lethal predation by epibenthic predators (de Vlas 1985).

In our first experiment, more clams adopted suspension feeding when additional food (cultured algae) was added to the water and those clams buried significantly deeper in the sediment than the clams supplied with natural and filtered estuarine water (Fig. 4). When different densities of suspension feeding *M. arenaria* were confined with *M. balthica*, the group without *M. arenaria* had significantly more food available in the water column as indicated by higher chlorophyll a concentration. This group has higher proportion of the clams utilizing suspension feeding. The presence of another suspension-feeding clam *Rangia cuneata* (Sowerby) resulted in reduction of food abundance in the water column and concomitant increase of deposit-feeding by *M. balthica* in a recent study conducted in North Carolina, USA (G. A. Skilleter, pers. comm.). However, in mixed populations of *M. balthica* and the suspension-feeding bivalve, *Cerastoderma edule* (L.), there was no clear influence of each other's growth and survival in a recent field study conducted at an estuary in Wadden Sea (Kamermans et al. 1992). In our experiment, although there was a trend for *M. balthica* with high density of *M. arenaria* to bury at a shallower depth than those with low or zero *M. arenaria* (Fig. 5), the difference among the three groups was not significant. This lack of significance could be a simple case of low power in the statistical test. An a posteriori analysis (Cohen 1969) showed that, even accepting a Type II error of 0.2, our experiment had the power to detect difference among treatments only when those differences exceed 1.7 standard deviation of the variation within them, i.e., about 4.3 cm. *M. arenaria* and *M. balthica* might feed on different components of suspended food particles in terms of size and/or composition, therefore the intensity of interspecific competition for food was small. We only measured concentrations of

particles smaller than 100 μm and did not examine the composition of the particles in the water column. Although *M. balthica* shows a linear relationship between the maximum size of particles which can be inhaled and animal shell length (Brey 1991), it does not select particles of a certain size (Self and Jumars 1988) and is able to ingest particles of a wide size range: from bacteria of only 1 to 2 μm (Harvey and Luoma 1984) to sand grains of ca. 300 μm (Gilbert 1977). *M. arenaria*, with its large siphon, should be able to filter an even wider size range of particles. Little is known about the food selectivity of these two species. Fluctuations of growth and condition in *M. balthica* correlated well with those of chlorophyll a in the water column (Thompson and Nichols 1988) and of planktonic diatoms, but not with flagellates (Beukema and Cadée 1991).

In the experiment testing the effects of intraspecific competition, the four-fold increase in clam density (from five to 20 per bucket) consistently, although not often significantly, resulted in a decrease in the abundance of suspended particles. Burial depth of the low density group was significantly deeper than those of medium and high density treatments (Fig. 7), although the proportion of clams adopting a deposit-feeding mode were not significantly different among the three treatments. We did not find any evidence of siphon interference during our observation, even in the clams of high density. The proportion of deposit-feeding individuals with large feeding radius (> 1 cm) seemed to be higher for the clams of medium and high densities than those of low density, although the difference was not significant due to large variations. In addition, we used 1 cm as the criterion for distinguishing large and small feeding radius without measuring actual length of the siphon extension. Large clams can take deposit up to at least 10 cm from their burrow (J. Lin, pers. observ.), more than the maximal distance (4 to 6 cm) previous workers found (Brafield and Newell 1961, Gilbert 1977). Therefore there was substantial variation in the length of siphon extension. The area of sediment surface swept clean by inhalant siphon of *M. balthica* increased with feeding time and on average, a clam of 16.5 mm shell length cleans a area of 90 cm² in 24 h (Brey 1991). In the present study, average feeding radius might be larger for clams of the high density group because of the more intensive competition for food. The larger feeding radius would be expected to result in shallower burial depth, as found in another tellinid clam *Scrobicularia plana* (da Costa) (Zwarts 1986).

Complex trophic interactions often have strong direct and indirect effects on marine community structure (e.g. Paine 1966, Simenstad et al. 1978, Posey and Hines 1991). Feeding of infaunal bivalves can exert pervasive effects both on their soft-bottom communities as dominant "functional groups" (Rhoads and Young 1970, Woodin 1976) and on the overlying planktonic communities through "benthic-pelagic coupling" (Dame et al. 1980). Deposit- and suspension-feeding bivalves may markedly

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affect community composition indirectly by regulating sediment stability (Rhoads 1974, Brenchley 1982) and biodeposition (Haven and Morales-Alamo 1972), as well as through adult-larval interactions (Woodin 1976). Suspension-feeding bivalves can limit the abundance of phytoplankton in the water column (Cohen et al. 1984, Nichols 1985, Alpine and Cloern 1992). Although predicting these community effects depends on accurately describing a species' feeding behavior, narrow categorization of feeding modes maybe difficult and misleading (Hines et al. 1989, Posey 1990). Our experiments here indicate that facultative switching between feeding modes in *M. balthica* is directly affected by both food availability in the over-lying water and indirectly by inter- and intra-specific competitors for that food resource. In turn, changes in feeding mode directly affects clam burial depth, and indirectly probably affects clam vulnerability to lethal predation and non-lethal siphon browsing by fish and decapods. For *M. balthica* as an abundant and widely distributed species in shallow boreal-cold temperate benthic communities, facultative switching between deposit and suspension feeding can have significant interactive consequences for marine and estuarine food web structure.

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