Contrasting influences of suspension-feeding and deposit-feeding populations of *Macoma balthica* on infaunal recruitment

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ABSTRACT: Effects of adult density of the bivalve *Macoma balthica* (L.) on growth and density in juvenile *M. balthica* (1 to 5 wk) was tested experimentally in the field (exclusion cages) and in the laboratory. Growth of juveniles was reduced in the presence of adults at normal field density in a sublittoral, sheltered, muddy-sand sediment but was not reduced under similar conditions in a sublittoral, wave-exposed, sand sediment. Density of juveniles was not affected by adults in either habitat, or in the laboratory. Growth reduction in juveniles at normal clam densities in the muddy sand habitat (where adults and juveniles are deposit feeders) but not in the sand habitat (where adults are suspension feeders and juveniles deposit feeders) indicates that intraspecific competition between adults and juveniles increases with increasing levels of dietary resource overlap between them. Density and growth of other species, both juveniles and adults, were not affected by the normal density of adult *M. balthica*. Increased competition between species with greater resource overlap was further indicated by the negative effect on densities of deposit-feeding *Hydrobia* spp. caused by very high experimental densities of adult *M. balthica* (deposit-feeding) in the muddy sand habitat, whereas deposit-feeding oligochaetes in the sand habitat reached their highest densities at the highest density of adult *M. balthica* (suspension-feeding). The laboratory experiments showed that the presence of a nereid polychaete reduced survival of juvenile clams. The different influences of polychaete and adult clams on juveniles suggest that a different level of interaction occurs between the 2 groups, i.e. a direct impact (predation, disturbance, interference competition) of polychaetes and an indirect impact (exploitation competition) of bivalves on juveniles.

INTRODUCTION

Interference of established adults with the recruitment of juveniles has been suggested to play an important role in regulating densities of soft-bottom marine invertebrates (Segerstråle 1962, Thorson 1966, Mileikovsky 1974, Woodin 1976, Peterson 1979). Early support for such adult-juvenile interactions (sensu Woodin 1983) came from field studies revealing a negative correlation between densities of juvenile and adult cockles (Thamdrup 1935, Smidt 1944, Kristensen 1957, but see Kreeger 1940). Later field experiments (e.g. Brock 1980, Williams 1980a, b, Levin 1981, Peterson 1982, Kent & Day 1983, Möller 1986, Crowe et al. 1987, Hunt et al. 1987), and laboratory studies (Woodin 1974,

Roe 1975, Tamaki 1985, Elmgren et al. 1986) have confirmed the existence of such an inhibitory effect. Woodin (1976) believed that adult-juvenile interactions determine the structure of dense suspension- and deposit-feeding bivalve populations.

According to Woodin (1976), adults inhibit larval recruitment in suspension-feeding populations by filtering larvae out of the water prior to settlement. She also maintained that in deposit-feeding populations the adults ingest or disturb larvae by their feeding activities. Therefore, such populations should undergo cycles (i.e. be age-class dominated) where low adult densities are a prerequisite for successful recruitment and where longevity of adults determine the frequency of these cycles. Gray (1981), criticizing this model, argued that the age-class phenomena often documented in bivalve populations cannot be explained by adult-juvenile interactions but result from poor recruitment years which in turn are linked with climatic

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variations. Various field experiments have been re-
ported to contradict as well as to support these
hypotheses (e.g. Wilson 1981, Gallagher et al. 1983,
Weinberg 1984, Oliver & Slattery 1985, Tamaki 1985).
A source of confusion in this context is how to define
'dense' assemblages (c.f. Gallagher et al. 1983). There-
fore, the final evaluation of the model will have to await
experimental tests of the influence of adults on juve-
niles over a wide range of densities in different popula-
tions and communities.

In a previous paper ('Olafsson 1986), I demonstrated
that 2 populations of *Macoma balthica* differ in their
feeding modes between habitats. One population, in a
sublittoral, sheltered, muddy-sand sediment, is primar-
ily deposit-feeding while the other population, in a
sublittoral, wave-exposed, sandy sediment, is primarily
suspension-feeding. *M. balthica* is known to ingest
particles as large as 0.3 mm (Gilbert 1977). At my study
sites, *M. balthica* larvae usually settle at a size of less
than 0.3 mm (unpubl.); thus it is possible for adult *M.
balthica* to filter these larvae out of the water prior to
settlement. Gallagher et al. (1983) argued that the
activity of the inhalant siphon of *M. balthica* during
deposit-feeding is sufficiently disturbing to cause
emigration of tanaids. This suggests that siphon activ-
ity of adults may also disturb juveniles. Therefore, adult
M. balthica in both suspension- and deposit-feeding
populations are potential inhibitors of recruiting *M.
balthica* larvae and juveniles. In the study described
here, I tested the effects of adults on juveniles over a
wide range of adult densities in both a suspension- and
a deposit-feeding population of *M. balthica*. In addi-
tion, I examined the effects of adults, over the same
range of densities in the 2 populations, on several other
dominant species in the 2 habitats.

MATERIALS AND METHODS

Study sites. Two localities were chosen. one on each
side of the Falsterbo Peninsula (55° 25' N; 12° 55' E), in
southern Sweden. Site A is a sheltered bay, where the
water masses are either stagnant or move slowly over
rich *Zostera* beds. The impact of wave action on the
sediment is small. The sediment at the experimental
depth (4 m) is thus relatively stable and consists of
muddy-sand (mean grain diam. = 0.11 mm, ignition
loss = 2.5 %). Besides *Macoma balthica* (L.), the only
other common macrobenthic species were the polyaete
Nereis diversicolor (Müller) (300 to 1400 m^{-2}), the gas-
tropod *Hydrobia* spp. (10000 to 40000 m^{-2}), the
amphipod *Microdeutopus gryllotalpa* (Costa) (500 to
1200 m^{-2}) and the cockle *Cardium hauniense* (Petersen
& Russell 1971) (200 to 1000 m^{-2}) (see 'Olafsson 1988).
Site B is an exposed sandy shore where the Baltic

current ensures rapid water exchange. Wave action
exerts strong influence on the sediment. The sediment
at the experimental depth (5 m) is thus unstable and
consists of fine-to-medium sand (mean grain diam. =
0.18 mm, ignition loss = 0.25 %). The only other abun-
dant macrobenthic species were the polychaete *Pygos-
pio elegans* (Claparede) (1000 to 15 000 m^{-2}), *Hydrobia*
spp. (1000 to 4000 m^{-2}), and the amphipod *Bathyporeia
pilosa* (Lindstrom) (400 to 2300 m^{-2}) (see 'Olafsson
1988). Salinity regimes were similar at both sites (8 to
10‰), but summer temperatures were somewhat
higher (19° vs 15°C) at Site A owing to the greater
stability of the water masses.

Caging experiments. The normal field abundance of
adult *Macoma balthica* (examined for longer than 1 yr)
is ca 1000 ind. m^{-2} in the muddy sand habitat and
250 ind. m^{-2} in the sand habitat ('Olafsson 1986).
Experimental densities were manipulated around these
natural levels. In the muddy-sand, I varied adult
densities from 250 (¼ normal field density) to 4000 (4 ×
normal field density) clams m^{-2} by stocking 5 cages
with respectively 25, 50, 100, 200 and 400 clams (clam
length = 0.5 to 1.4 cm). In the sand site, I varied adult
densities from 100 (ca ½ × normal field density) to 1000
(4 × normal field density) clams m^{-2} by stocking 4
cages with respectively 10, 25, 50 and 100 clams (clam
length = 0.5 to 1.7 cm). A cage consisted of a solid box
with a net top. The box, made of PVC, was 0.1 m^2 in
area (sides = 31 × 32 cm, height = 15 cm). The top
covering the box was 30 cm high and constructed of
2.5 mm fiberglass mesh strengthened with PVC ribs.
Each box was completely buried in the sediment, and
only the 30 cm high net top was visible above the
sediment surface. These tops allowed all of the previ-
ously listed species in this community (except adult *M.
balthica*) to move freely into and out of the cages and
also facilitated water circulation.

The experiment was initiated on 27 April 1983 in the
sand site, 29 April 1983 in the muddy-sand site; it was
terminated in early July (6th in the sand site, 8th in the
muddy-sand site). Settlement of *Macoma balthica* lar-
vae usually occurs during June; hence the experiment
was started well before the beginning of settlement.
Meiofaunal samples within cages (15 cores cage^{-1})
were collected by divers using a core sampler
(4.52 cm^2). The core was pressed 2 to 2.5 cm into the
sediment, and each corer was then emptied on the spot
into small plastic jars. Thus, I used 1 cage per density of
adult *M. balthica* in each habitat and subsampled (15
samples) each cage when terminating the experiment.
In the laboratory the contents of each jar were individu-
ally passed through a 0.08 mm sieve. The sieve
residues were then preserved in 70 % ethanol and
stained with rose bengal. Animals were sorted, iden-
tified, counted, and measured in the laboratory I only

counted juveniles of high-abundance species to avoid samples with zeros in the analyses. This is why *Hydrobia* spp. were counted in samples from the muddy-sand but not from the sand site, and oligochaetes were counted in the sand site but not in the muddy-sand site. *Hydrobia* spp. and oligochaetes were not separated into adults and juveniles. However, considering the duration of the experiment it is probable that these species entered the cages as juveniles. Also *Cardium glaucum* Bruguiere occur in high abundance as juveniles (but not as adults) in both experimental sites, whereas *C. hauniense* (both adults and juveniles) only occur in the muddy-sand site. Thus, whereas the sand site contains only 1 species of *Cardium*, the muddy-sand site probably contains 2. Size of juvenile *M. balthica* and juvenile *C. glaucum* was measured to the nearest 0.02 mm using a dissecting microscope and an ocular micrometer.

Laboratory experiments. Experiments designed to test the influence of adult *Macoma balthica* and *Nereis diversicolor* on juvenile *M. balthica* were carried out in June–July 1985. Substrate from the sheltered habitat was strained through a 0.5 mm sieve and flushed with 70 °C tap water for 3 h to kill meiofauna. This substrate was then placed in cores so that each core contained a 9 to 10 cm thick sediment layer. The cylindrical cores were 10 cm in diameter and 18 cm deep. Fifteen cores were placed in an open box in a 3×5 matrix. I used one matrix for the *M. balthica* experiment and one for the *N. diversicolor* experiment. Water entered each core from holes (of the same size = 1 mm diam.) in a system of tubes above the cores and exited through 3 holes (2 cm diam.) placed 3 cm below the top of each core. Holes were covered with a nylon net (0.5 mm mesh) to prevent adults from escaping. Flow through the system was maintained with water from the channel outside the field station. The water was not recirculated and

had the same salinity as water at the study sites (8 to 10‰).

Intraspecific effects of different densities of adult *Macoma balthica* on the density of juveniles were tested by stocking cores with various numbers of adult clams (ranging from 0 to 24 clams $core^{-1} = 0$ to 3055 clams m^{-2}) and a constant number of newly settled (0.250 to 0.300 mm) juveniles (Table 4). Similarly, the effect of different densities of adult *Nereis diversicolor* on the density of juvenile *M. balthica* was tested by stocking cores with various numbers of adult *N. diversicolor* (ranging from 0 to 40 polychaetes $core^{-1} = 0$ to 5100 polychaetes m^{-2}) and a constant number of juvenile bivalves. Three replicates of each treatment were allowed to run for 15 d.

I used simple regression analysis to test for effects of adult *Macoma balthica* density on density and growth (size) of juveniles. The stepwise change in e.g. size of juvenile bivalves and density of *Hydrobia* spp. in the muddy-sand site (Tables 1 and 3) with increasing density of adult bivalves suggests an exponential rather than a straight-line relationship between these variables. Therefore, the data were transformed to ln (x) (density of adult *M. balthica* and size values) and ln (x+1) (density of juveniles) before running analyses. If a significant ($p < 0.05$) R-value resulted from the regression test, and a posteriori test (Tukey) was used to determine which means differed from each other ta(after running a 1-way ANOVA).

RESULTS

In the muddy-sand habitat, the size of juvenile *Macoma balthica* was clearly dependent on adult density (Table 1, $N = 163$, $R = -0.368$, $p < 0.001$; ANOVA, $p < 0.001$). A pronounced decline in juvenile

Table 1. *Macoma balthica*. Size and density of juveniles (1 to 5 wk in the benthic stage) in cages with various densities of adults in muddy-sand and sand habitats. One cage per adult density in each habitat and each cage subsampled *(n)* at the end of experimental period

Adults Cage density (ind. m^{-2})	Juveniles Size (mm) $\overline{X} \pm SD\ (n)$	Density (ind. m^{-2}) $\overline{X} \pm SE\ (n)$
Muddy-sand habitat		
250	0.645 ± 0.162 (41)	6040 ± 1830 (15)
500	0.629 ± 0.198 (25)	3540 ± 699 (15)
1000	0.524 ± 0.096 (32)	4720 ± 944 (15)
4000	0.504 ± 0.077 (39)	5750 ± 1020 (15)
Sand habitat		
100	0.474 ± 0.078 (72)	17 100 ± 2926 (15)
250	0.486 ± 0.075 (73)	27 800 ± 4440 (15)
500	0.459 ± 0.067 (77)	23 100 ± 5370 (15)
1000	0.453 ± 0.067 (88)	19 900 ± 4560 (15)

size occurred when the density of adult clams was increased from 500 to 1000 m^{-2} (Table 1). Juvenile size differed by 38 % between the treatments representing the 2 extreme densities of adults (250 and 4000 clams m^{-2}, settling size = 0.28 mm). The a posteriori contrast showed differences in mean size of juvenile M. balthica between cages with 250 and 1000 m^{-2}, with 250 and 4000 m^{-2} and between cages with 500 and 4000 adults m^{-2} (Table 1). Density of juveniles was independent of adult density (Table 1, $N = 75$, $R = 0.06$, $p = 0.607$).

In the sand habitat, juvenile size was also reduced by adult density but less so compared with the muddy-sand habitat (Table 1, $N = 310$, $R = -0.133$, $p = 0.019$; ANOVA, $p < 0.01$). Juvenile size differed by 11 % in treatments representing the 2 extreme densities of adults, 100 and 1000 clams m^{-2}. The a posteriori test showed no differences in mean size of juveniles between cages. Juvenile density was independent of adult density (Table 1, $N = 60$, $R = -0.015$, $p = 0.909$).

In the muddy-sand habitat, the size (Table 2, $N = 239$, $R = -0.099$, $p = 0.127$) and density (Table 2, $N = 75$, $R = -0.44$, $p = 0.708$) of juvenile Cardium glaucum were independent of the density of adult clams. In the sand habitat also, the size (Table 2,

$N = 55$, $R = -0.14$, $p = 0.309$) and density (Table 2, $N = 60$, $R = 0.106$, $p = 0.422$) of juvenile C. glaucum were independent of adult clam density.

In the muddy-sand habitat, adult Macoma balthica density had a significant negative effect on the density of Hydrobia spp. (Table 3, $N = 75$, $R = -0.259$, $p = 0.025$; ANOVA, $p < 0.01$). The a posteriori test showed a difference in mean density of Hydrobia spp. between the cage containing 4000 and the cages containing 250, 1000 and 2000 adult clams m^{-2} (Table 3). In the sand habitat, adult clam density had a significant positive effect on the density of oligochaetes (Table 3, $N = 56$, $R = 0.36$, $p = 0.006$; ANOVA, $p < 0.001$). The a posteriori test showed a difference in mean density of oligochaetes between the cage with 1000 and the cages with 100 and 500 adult clams m^{-2}.

No significant effect of adult Macoma balthica density on density (= mean density of juveniles, stocked + recruits during the experiment, over 3 replicates) of juvenile M. balthica was found in the laboratory experiments (Table 4, $N = 15$, $R = -0.362$, $p = 0.185$). However, density of adult Nereis diversicolor had a significant effect on the density of juvenile clams (Table 4, $N = 15$, $R = -0.804$, $p < 0.001$;

Table 2. Macoma balthica and Cardium glaucum. Size and density of juvenile (0 to 3 wk in the benthic stage). C. glaucum in cages with various densities of adult M. balthica in muddy-sand and sand habitats

M. balthica adults Cage density (ind. m^{-2})	C. glaucum juveniles	
	Size (mm) $\overline{X} \pm SD$ (n)	Density (ind. m^{-2}) $\overline{X} \pm SE$ (n)
Muddy-sand habitat		
250	0.498 ± 0.151 (33)	13 700 ± 1820 (15)
500	0.529 ± 0.189 (56)	20 200 ± 4860 (15)
1000	0.548 ± 0.182 (46)	17 200 ± 4730 (15)
2000	0.545 ± 0.152 (56)	23 400 ± 6990 (15)
4000	0.439 ± 0.157 (48)	12 400 ± 2660 (15)
Sand habitat		
100	0.416 ± 0.132 (14)	3090 ± 915 (15)
250	0.452 ± 0.128 (20)	3390 ± 769 (15)
500	0.382 ± 0.107 (10)	5300 ± 1090 (15)
1000	0.371 ± 0.085 (11)	4570 ± 1780 (15)

Table 3. Density of Hydrobia spp. and oligochaetes in cages with various densities of adult Macoma balthica in muddy-sand and sand habitats

Muddy-sand habitat		Sand habitat	
Cage density of adult M. balthica (clams m^{-2})	Density of Hydrobia spp. (ind. m^{-2}) $\overline{X} \pm SE$ (n)	Cage density of adult M. balthica (clams m^{-2})	Density of oligochaetes (ind. m^{-2}) $\overline{X} \pm SE$ (n)
250	15 800 ± 2120 (15)	100	15 800 ± 3130 (14)
500	11 800 ± 2150 (15)	250	23 900 ± 5610 (15)
1000	15 800 ± 1870 (15)	500	12 900 ± 2540 (12)
2000	15 700 ± 1710 (15)	1000	42 400 ± 6520 (15)
4000	7 660 ± 1300 (15)		

Table 4. *Macoma balthica*. Density of juvenile (initially 50 per 78.5 cm^2 core + juveniles settling in cores during experiment) exposed to various densities of (a) adult *M. balthica* and (b) *Nereis diversicolor*. All treatments replicated 3 times

No. ind. aquarium^{-1}	Survival of juvenile *M. balthica*	
	$\overline{X}$	SD
(a) 0 adult *Macoma* + juveniles	82	39
3 adult *Macoma* + juveniles	78	62
6 adult *Macoma* + juveniles	50	22
12 adult *Macoma* + juveniles	57	33
24 adult *Macoma* + juveniles	47	8
(b) 0 adult *Nereis* + juveniles	106	39
5 adult *Nereis* + juveniles	38	11
10 adult *Nereis* + juveniles	38	2
20 adult *Nereis* + juveniles	46	25
40 adult *Nereis* + juveniles	33	7

ANOVA, $p < 0.01$). The a posteriori test showed no differences in density of juvenile clams between treatments. However, there was a marked difference in density (but not significant) of juvenile clams between cores with and without polychaetes but not between cores with different densities of polychaetes, indicating that only the presence but not density of *N. diversicolor* had an effect on the density of juvenile clams (Table 4). An increase in juvenile clams during the experimental period possibly introduced a bias into the laboratory experiments (Table 4). The larvae apparently entered with fresh seawater and settled in the aquaria. However, the amount of incoming water was not likely to differ much between treatments, and the tube system probably helped create a uniform distribution of larvae in the water before they reached the cores. Therefore, it seems reasonable to assume an even distribution of larvae among treatments within each matrix (differences between matrices may have arisen due to the fact that they were coupled in series with water pressure being reduced along the system). Hence, the initial density of juvenile clams was based on levels measured in aquaria without adults.

DISCUSSION

My field experiments showed that densities of juvenile *Macoma balthica* and juvenile *Cardium glaucum* were unaffected by the density of adult *M. balthica* in both habitats (suspension- and deposit-feeding). The laboratory experiment confirmed this result. Adult *M. balthica* exhibit a strong growth reduction in the deposit-feeding population at densities of 1000 adults m^{-2} and a weak growth reduction at the same density in the suspension-feeding population ('Olafsson 1986, 1988). These observations were interpreted as a result of competitive interactions for food or space ('Olafsson 1988). I consider a density at which

adults compete for food or space to be an adequate definition of a 'dense' population in the context of adult-juvenile interactions. Also, this definition seems to be close to what Woodin (1976) means by a 'dense' assemblage, although she does not present a clear definition of this term. Provided that my assumption is right, then the above results impose limitations to, or modifications (see Commito 1987) of, Woodin's (1976) general suggestion that dense populations of adult suspension-feeders (by inhibiting larval settlement) and deposit-feeders (by reducing juvenile survival) *effectively* inhibit recruitment.

Growth of juvenile *Macoma balthica* was reduced by adult conspecifics at natural densities in the muddy-sand habitat (1000 ind. m^{-2}) but not in the sand habitat (250 ind. m^{-2}). Differences in juvenile size between habitats may be due to differences in settling time, temperature, or food abundance. However, within habitats differences in size are probably due to differences in growth rate, since settling time presumably is uniform. Thus, adult density influences juvenile growth rate in the muddy sand habitat. However, in order to support Woodin's (1976) predictions, the demonstrated effects need to be asymmetric, i.e. adults (i) must have a greater impact on juveniles (j) than juveniles have on adults (when $a_{ji} > a_{ij}$). Such an effect may eventually lead to increased mortality of juveniles. No such effect could be demonstrated since both adults and juveniles showed decreased growth rates at high adult densities (see also 'Olafsson 1986). In this situation the relative effects are difficult to estimate as the relationship between size and growth in molluscs is complex (Peterson & Andre 1980). Consequently, asymmetrical effects are best measured as differences in survival through time between adults and juveniles. The observation that growth of juvenile clams was seriously inhibited in the muddy sand habitat without any accompanying reduction in survival supports my earlier interpretation ('Olafsson 1986), that the cause for growth reduction in

this population (in both adults and juveniles) was mainly exploitative competition. A similar result was obtained by Williams (1980a), who observed a reduction in growth of juvenile Manila clams living together with high densities of adults without any accompanying reduction in survival after 9 mo. Peterson (1982) also showed a similar pattern for *Chione undatella*. I have therefore concluded that my experiments demonstrate a strong intraspecific competition for food at normal clam densities in the muddy-sand habitat. However, until this experiment has been repeated over a longer time period, which would also take mortality effects into account, the influence of adults on recruitment (settlement to age 1 yr, see 'Olafsson 1988) in this population will be difficult to evaluate.

The density effect of adult *Macoma balthica* on juvenile *Cardium glaucum* and on juvenile *M. balthica* seems to differ in strength. In the muddy-sand habitat, growth of juvenile *C. glaucum* was not reduced by the experimental densities of adult *M. balthica* (with a possible exception for the highest experimental density of adult clams = 4000 ind. m^{-2}), whereas a strong effect on juvenile clams was observed at normal adult densities (1000 ind. m^{-2}). The differences may be attributable to different feeding modes. Juvenile clams are obligate deposit feeders, using their ciliated foot as a feeding organ (Caddy 1969), whereas juvenile *Cardium* are filter feeders (Lebour 1938, Creek 1960). Food overlap between adult and juvenile clams, which are both deposit feeders, is presumably greater than between adult *M. balthica* and juvenile *C. glaucum* (a deposit feeder and a suspension feeder). According to niche theory, intraspecific competition for food should be greater than interspecific competition in this case (MacArthur & Levins 1967, review in Schoener 1983).

At peak experimental densities of adult clams, *Macoma balthica* seemed to influence densities of several other species, i.e. *Hydrobia* spp. in the muddy-sand habitat and oligochaetes in the sand habitat. Both these effects were observed in only one cage which calls for some caution when interpreting the results. However, both effects have been demonstrated experimentally in other studies. *Hydrobia* spp. emigrate in response to extreme crowding and other unfavourable conditions (Levinton 1979). Since hydrobiids are deposit feeders, and therefore presumably compete with adult *M. balthica* in this habitat, increased competition for food could probably explain the reduction in *Hydrobia* density at this artificially high clam density. In contrast, the deposit-feeding oligochaetes in the sandy habitat showed their highest density in the treatment with the highest density of adult clams. High meiofaunal abundance associated with high clam densities has previously been reported (Reise 1983), and Commito & Boncavage (1989) showed that the

oligochaete *Tubificoides benedeni* increased in density in response to increasing densities of the suspension feeder *Mytilus edulis*. My experiment suggests that the suspension-feeding *M. balthica* transfers energy from the water column to the sediment where it is manifested as an increase in food supply for deposit-feeding oligochaetes. Frithsen & Doering (1986) also showed that the suspension-feeding activity of spionids could affect water-column particle dynamics and suggested that such activity may increase sedimentation of organic detritus bringing about high concentrations of such material in localized areas. These results support the hypothesis of Dame et al. (1980) that suspension feeders can be important in the coupling between water column and benthic subsystems (but see Black & Peterson 1988). Also, this result supports Gallagher et al. (1983), who believed that facilitation can be as equally an important factor as inhibition in soft-substratum community succession.

Nereis diversicolor is abundant at the sheltered site, and 'Olafsson & Persson (1986) showed that this polychaete, by way of disturbance, may be a strong structuring force in muddy-sand communities (see also Ambrose 1984). Thus, among the species in this community, *N. diversicolor* was considered to be the most likely candidate to influence infaunal recruitment. *N. diversicolor* also showed a significant effect on survival of juvenile *Macoma balthica*. Although not significant, a difference in densities occurred between cores with no polychaetes and cores containing polychaetes. Thus, the response did not seem to be density-dependent. Such absence of, or weak, density-dependence in interactions between adult polychaetes and juvenile macrofauna was also observed by Whitlatch & Zajac (1985) and Luckenbach (1987).

Experimental studies in marine soft sediments on adult-juvenile interactions have been concerned with bivalves (Brock 1980, Williams 1980a, b, Peterson 1982, Bonsdorff et al. 1986, Möller 1986), polychaetes (Woodin 1974, Roe 1975, Weinberg 1979, 1984, Wilson 1980, Levin 1981, Kent & Day 1983, Tamaki 1985, Rönn et al. 1988), and crustaceans (Highsmith 1982, Oliver & Slattery 1985, Elmgren et al. 1986). General trends relevant in the present context, are: (1) The impact of polychaetes on juveniles exceeds that of bivalves. This difference was apparent in my laboratory experiments and may reflect differences in the type of interactions between adults and juveniles – i.e. indirect (exploitative competition) interactions in bivalves and direct (predation, disturbance, interference competition) interactions in polychaetes. A similar pattern, i.e. polychaetes showing stronger negative influence on juvenile polychaetes than other species, was observed by Whitlatch & Zajac (1985). (2) The documented effect is stronger in laboratory studies than in field studies. (3)

In field experiments differences between treatments tend to decrease with time (Williams 1980a, Peterson 1982, Kent & Day 1983). This may cause the difference described in (2). However, if adult-juvenile interactions are to be considered as important structuring forces, their influence must be demonstrated over time intervals longer than just a few weeks. In manipulatory studies it is easy to emphasize the importance of one factor in the regulation of the population or community studied (cf. Woodin 1983). However, a documented adult-juvenile effect must be evaluated together with other possible effects (e.g. mobile epibenthic predation, Brock 1980, Möller 1986; impact of meiofauna, Williams 1980a, Watzin 1983, 1986) to determine its actual impact on population or community structure.

Hurlbert (1984), in a seminal paper, pointed out the pitfalls with pseudoreplication in ecological experiments. This is not a critical issue for my interpretations: (a) Provided that adult *Macoma balthica* do not influence initial recruitment of the species included in this study the 5 cages at the sheltered site and the 4 cages at the wave-exposed site are 'true' replicates. The point here is that one can usually make stronger conclusions from data that show absence of impact than data that show impact. This point is well illustrated in my data set. Juvenile bivalves show a uniform distributional pattern among cages and are therefore ad hoc replicates indicating absence of adult influence. *Hydrobia* spp. and oligochaetes on the other hand differ in their pattern of abundance, and both show a response to adult density in only 1 cage out of 3 in the wave-exposed site and 4 in the sheltered site. Although the pattern in both these cases is readily explained in terms of biological logic, that both types of interactions have been repeated in other experiments and that the probability is very low that chance effects may have created the observed pattern, these data must be treated with caution. (b) If Woodin's (1976) hypothesis is true, then 'gross effects of treatments are anticipated' (see Hurlbert 1984), i.e. an efficient inhibition of initial recruitment is anticipated. The data do not indicate any such effect. On the contrary, the data indicate a uniform recruitment into the cages at boh study sites. There is of course always the possibility that a cloud of high-density larvae settled into cages with high densities of adult *M. balthica*. This is conceivable in the wave-exposed site since I had only 1 cage with the stated critical density (1000 adults m^{-2}) at this site, but hardly at the sheltered site where there were 3 cages at and above this density. However, Woodin's hypothesis does not incorporate variation in settlement. It states that very few larvae enter the benthic stage in dense suspension-feeding populations and few juveniles survive the early benthic phase in dense deposit-feeding populations. My data contradict these predictions.

In summary, the results presented here indicate: (1) Adult *Macoma balthica* vary in their effect on juveniles depending on their habitat and feeding mode. (2) Inhibition of growth may occur without any clear effect on density. (3) Intraspecific competition is stronger than interspecific competition in the muddy-sand habitat (see also 'Olafsson 1986). (4) Competition is stronger in deposit-feeding communities than in suspension-feeding communities (cf. Levinton 1972, 'Olafsson 1986). (5) Dense populations of adult *M. balthica* do not effectively reduce survival of juvenile conspecifics during settlement and their first weeks in the benthic stage, i.e. during the time which juveniles presumably are most vulnerable to the type of adult-juvenile interactions suggested by Woodin (1976).

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