

Biotic enrichment of intertidal sediments by experimental aggregates of the deposit-feeding bivalve *Macoma balthica**

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ABSTRACT: Experimental aggregates of the bivalve *Macoma balthica*, established on a sandy tidal flat in the North Sea, are preferentially colonized by small zoobenthos. The tellinids stay buried at 3 to 6 cm while their long inhalant siphons pick up deposits from the surface. The short exhalant siphons terminate within the sediment. High abundance of diatom-feeding Turbellaria at the surface, and bacteria-feeding and predatory species in the subsurface suggest enhanced growth of microalgae, bacteria and their grazers, stimulated by *M. balthica*. No such 'gardening' effects are observed within aggregates of the suspension-feeding cockle *Cerastoderma edule*, where exhalant siphons are flush with the surface. Both bivalve aggregates, however, displaced the tube-dwelling polychaete *Pygospio elegans*.

INTRODUCTION

The ecological role of organisms cannot be measured solely in terms of their population metabolism. Organisms may also exclude or promote co-existing species. Such effects can be demonstrated in field experiments, where representatives of one species are added or removed and the effect on co-existing organisms are recorded. In this study, I added 2 bivalve species to tidal-flat sediments in the North Sea – representatives of a deposit feeder and a suspension feeder – in order to determine which one exerted more effects on other benthos forms. Do negative effects (competition, food depletion) prevail or are there any positive effects when bivalves arrange in dense assemblages?

Instead of sampling the entire benthos, I singled out Turbellaria and small Polychaeta because of their high number of species, extended vertical ranges in the sediment, and diverse modes of feeding. Particularly in Turbellaria, the gut content is readily visible and species could be assembled into 3 trophic guilds based on observations on the experimental site: bacteria-feeders, diatom-feeders and predators. Turbellaria and small Polychaeta are taken as bioindicators for the

general effects of the experimental addition of bivalves on the tidal flat benthos. At the site these taxa comprise 11 % and 4 % of all Metazoa, respectively.

One polychaete species suffered competitive displacement while another polychaete and all Turbellaria became more abundant when the deposit-feeding bivalve was added. The trophic guilds of Turbellaria suggest that the deposit-feeding bivalve is 'gardening' its own food source. The suspension-feeding bivalve displaced the same polychaete but had no positive effects on other benthos at the experimental site. In marine benthos, Hylleberg (1975) was the first to introduce the concept of gardening, and Gerlach (1978) suggested that it applies to interactions between zoobenthos and bacteria in general.

MATERIAL AND METHODS

Habitat

The experiments were done on a bare, sandy tidal flat ('Königshafen') at the eastern coast of the North Sea, close to the island of Sylt. Depth at high tide is 1.6 m. Exposure to air is about 2 h per tidal cycle (semilunar). Annual mean water temperature is 10 °C

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(summer 15.1, winter 4.5 °C). Salinity remains close to 31 ‰. Sand grains are mainly quartz with a median of 0.46 mm ($\phi = 1.14$) and a sorting coefficient of 1.5. Organic content is 0.4 % (dry weight).

The flat is dominated by the lugworm *Arenicola marina* L. (60 ind. m⁻²). Numerically, Nematoda are most important (11 10⁵ · m⁻²) and primarily live in the upper 3 cm of sediment. In July/August 1981, the sediment was oxidized in the upper 0.5 cm, below it was black.

Experiments

The tellinid *Macoma balthica* (L.) lives buried in the sediment at 3 to 6 cm depth, and a long inhalant siphon is extended up to the surface where food particles are gathered. I collected 148 individuals with an average length of 12 mm (range 7 to 15 mm; mean volume 0.3 cm³), washed them to remove adhering small fauna, and assembled them into 4 equal groups. These groups were transplanted into sediment, allowing 3 cm² for each individual. To accomplish this without disturbing the sediment, I excavated sediment cores of 110 cm² and 11 cm depth during low tide, cut off the top at 3.5 cm, placed 37 tellinids evenly on the cross section, and then replaced the top layer.

When collecting *Macoma balthica*, I noted that most were oriented more or less horizontally in the sediment, lying on their left side. In the Experiment I oriented them accordingly. Finally, the entire cores were fitted into appropriate containers made out of gauze (mesh size 1 mm), open to the surface, and then were placed back into the tidal flat sediment. With 4 controls I did exactly the same but left out the tellinids.

A similar experiment was done with the suspension-feeding cockle *Cerastoderma (Cardium) edule* (L.). Its siphons are short and apertures are flush with the surface. I collected 106 cockles with an average length of 18 mm (range 11 to 21 mm; mean volume 2 cm³; age 2 yr), assembled them into 4 groups of 26 and 27 individuals, and placed them on areas of 110 cm², allowing 4 cm² for each cockle. Each area was surrounded by an anchored PVC-ring, flush with the sediment surface. All cockles quickly buried themselves. As controls, I placed 4 rings on the sediment, and made sure that no cockles were inside by raking the sediment with a finger.

Sampling

Both experiments were started on July 23, 1981. The cockle experiment was terminated after 22 d, the tellinid experiment after 30 d. Of the 4 *Macoma*-aggre-

gates, 3 were sampled at the end of experiment. The fourth aggregate was used for pilot sampling and sediment analysis. I took 2 samples from each of 3 containers, together 6 controls and 6 from tellinid aggregates. Each sample was a sediment core of 2 cm² and a depth of 8 cm, divided into 1 cm intervals. Thus, a total of 96 2 cm³ units of sediment were transported to the laboratory where they were sorted with respect to Turbellaria and Polychaeta. All tellinids still present in the containers were counted.

The cockle aggregates were sampled similarly. However, depth of cores was limited to 2 cm because pilot sampling revealed no Turbellaria deeper than this. In the aggregates, cockle siphons were visible at the surface and I took each sample adjacent to a cockle. Numbers of *Cerastoderma edule* were counted.

RESULTS

In July 1980, a set of 6 parallel cores of 2 cm²/0–5 cm was taken, divided into 0.5 cm depth intervals. One core happened to include an individual *Macoma balthica* (11.5 mm long), positioned at a depth of 3.5 cm. In that core, the vertical distribution of meiofauna (including large ciliates) was quite different compared to the other 5 (Fig. 1). Close to the surface, total abundance was as usual. Below 2 cm depth, however, abundance of Ciliata, Nematoda and Turbellaria increased considerably and remained high to a depth of 4 cm, then abruptly decreased. In the other 5 cores, high abundance was limited to the upper 1.5 cm and then remained close to zero. The total abundance of small fauna below 2 cm² was 280 ± 49 in the 5 normal cores, and 987 in the presence of *M. balthica*, a 3.5 fold increase. This pilot investigation led to the following experiments.

Aggregates of *Macoma balthica*

Tellinids were experimentally arranged into 4 aggregates, each with 37 individuals below 110 cm². Gauze prevented lateral emigration but escape from the sediment was possible. This, or removal by predators, was negligible over the 30 d of experiment. I encountered 30, 32, 36 and 36 individuals in the 4 containers. All were alive. In the controls and the tellinid containers, the upper 0.5 cm of sediment were brownish (= oxidized). Below this, the sediment in the control containers was black (= reducing). In the tellinid containers, numerous pockets of brownish and grey colour occurred in the depth range of 2 to 6 cm. A 1 mm layer of brownish sediment surrounded most tellinids, and more extensive grey halos were always

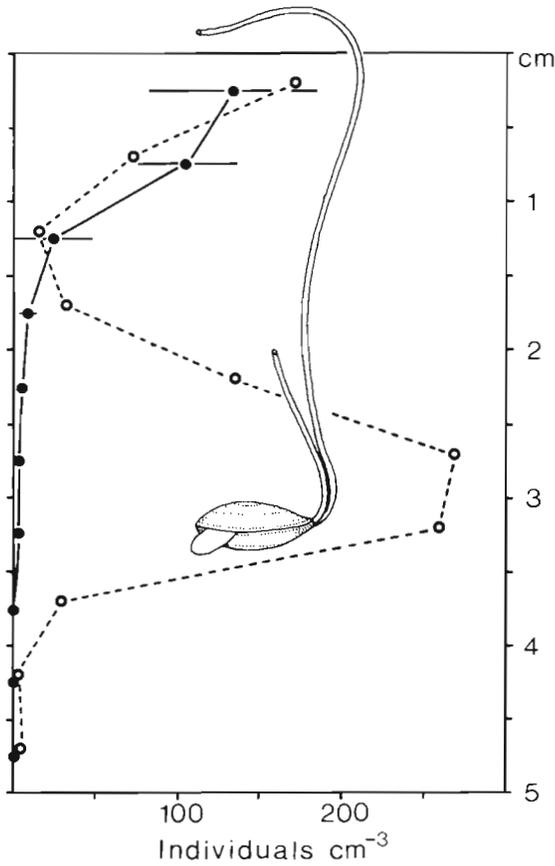


Fig. 1. Vertical distribution in 0.5-cm intervals of small zoobenthos abundance (including Ciliata > 0.2 mm length) in the upper 5 cm of normal sediment (mean and standard deviation of 5 cores of 2 cm²) and in a single core (broken line) which happened to include an individual of *Macoma balthica*, positioned at 3.5 cm depth

present. Frequently, siphons were found within brownish or grey sediment but they also ran through completely black zones.

Turbellaria show a preference for the tellinid aggregates (Table 1). The difference between controls and aggregates is most pronounced in the subsurface com-

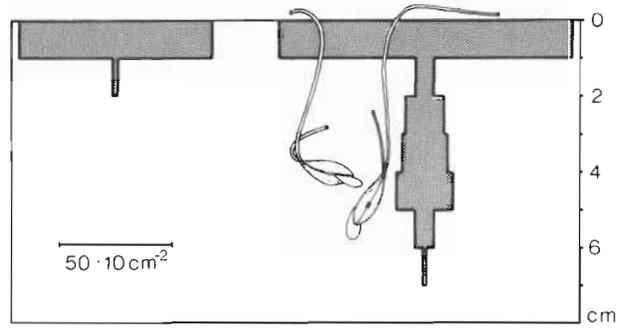


Fig. 2. Vertical distribution of turbellarian abundance in normal sediment and within experimental aggregates of *Macoma balthica* (right), positioned at 3 to 6 cm depth

ponent, but also at the surface Turbellaria are significantly more numerous within the experimental aggregates (Fig. 2). The same applies to species density and species richness. Other measures of diversity (Shannon-index, inverted Simpson-index, evenness) all tend to be lower within the tellinid aggregates. This is primarily due to 3 species achieving a strong dominance (together 54 %) within aggregates (Fig. 3), one at the sediment surface (*Macrostomum pusillum*), one over the entire vertical range (*Archilopsis unipunctata*), and one in the deep sediment (*Neoschizorhynchus parvorostro*).

All 3 trophic guilds of Turbellaria (bacteria-feeders, diatom-feeders, predators) contribute significantly to the increased abundance within tellinid aggregates (Table 1). Considering the upper 2 cm of sediment, only diatom-feeders are significantly more abundant. In bacteria-feeders and predators, it is primarily the subsurface component that contributes to the observed differences.

None of the turbellarian species is more abundant in the controls (Table 2). While diatom-feeders are confined to the sediment surface, many of the bacteria-feeders and predators colonize the subsurface when tellinids are present. The strong subsurface component

Table 1. Components of the turbellarian assemblage in the absence of and within aggregates of *Macoma balthica*. Means (SD = standard deviation) of 6 samples of 2 cm²/0–8 cm. P = probability of error when assuming higher values for Turbellaria in sediment with *M. balthica* (Mann-Whitney U-test)

Individuals 2 cm ⁻² (SD)	No <i>Macoma</i>	With <i>Macoma</i>	U-test P
All Turbellaria in 0 to 8 cm depth	17.3 (7.1)	41.7 (5.8)	< 0.01
in 0 to 2 cm depth	17.3 (7.1)	27.3 (7.4)	< 0.05
in 2 to 8 cm depth	0.0	14.4 (7.4)	< 0.01
Diatom-feeders (8 spp.)	7.5 (3.6)	12.5 (3.7)	< 0.05
Bacteria-feeders (5 spp.)	2.0 (1.1)	7.3 (2.7)	< 0.01
Predators (23 spp.)	7.7 (3.8)	21.0 (8.1)	< 0.01
Species richness (12 cm ²) in 0 to 2 cm	26	25	
in 0 to 8 cm	0	11	

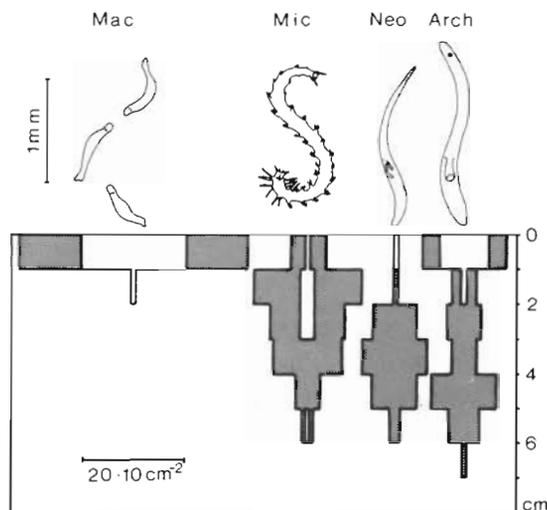


Fig. 3. Vertical distribution of species' abundances in normal sediment (white) and within aggregates of *Macoma balthica* (dark shaded with white areas inclusive). Light shading: layer where tellinids are positioned. Mac = *Macrostomum pusillum* (diatom-feeder), Mic = *Microphthalmus* 2 spp. (diatom- and bacteria-feeder), Neo = *Neoschizorhynchus parvorostro* (bacteria-feeder), Arch = *Archilopsis unipunctata* (predator)

of Turbellaria within the aggregates (Fig. 2 and 3) cannot be explained by simple downward migration from the surface layer. There are too few *Neoschizorhynchus parvorostro* at the surface to allow for the observed high numbers in 2 to 5 cm depth of aggregates. *Archilopsis unipunctata* increased in abundance at the surface as well as below. Nine turbellarian species of the subsurface component are completely missing at the surface. Immigration from external sources must be assumed.

Small Polychaeta also respond to the initiation of tellinid aggregates (Table 3). The interstitial *Microphthalmus sczelkowiei* populates the transition zone between surface and subsurface when *Macoma balthica* is present (Fig. 3). This hesionid polychaete feeds on bacteria and microalgae. The tube-dwelling *Pygospio elegans* is significantly less abundant within *Macoma*-aggregates. Similar to the tellinid, this spionid feeds on small particles collected from the sediment surface. Another tube-dwelling polychaete, *Spio filicornis*, is not affected. Species density is higher within the aggregates compared to the controls, while total species richness is similar.

Within 30 d, aggregates of *Macoma balthica* induced considerable increase in the abundance of the subsurface component of small Polychaeta and of Turbellaria, and in the latter group also in the surface component. Out of 48 turbellarian and polychaete species, only 1 significantly decreased in number within tellinid aggregates.

Aggregates of *Cerastoderma edule*

Most cockles moved out of the experimental aggregates within 22 d. Out of the 26 or 27 cockles initially assembled to each of 4 aggregates, only 11 in 3, and 8 in 1 were still present. The others crawled out and many of them were observed in the vicinity. Cockles generate no micro-oxic zones in the reduced subsurface sediment. Samples were taken from the 3 containers with 11 cockles each (1 cockle 10 cm^{-2}). Turbellaria remained indifferent to these experimental aggregates of *Cerastoderma edule* (Table 4). However, they are considerably more patchy in distribution between cockles than elsewhere (Lloyd's index of patchiness).

Of small Polychaeta, none is significantly more abundant within cockle aggregates (Table 5). *Pygospio elegans* is sensitive also to the presence of this bivalve and abandoned the aggregates. This also applies to all 3 tube-building spionids combined. Probably, the crawling of cockles is harmful to tube-dwellers.

DISCUSSION

Deposit-feeding in *Macoma balthica*

Macoma balthica is reported to utilize detritus, bacteria, diatoms and protozoans as food (Wernstedt, 1942; Fenchel, 1972; Tunnicliffe and Risk, 1977). Investigators disagree whether *M. balthica* is an obligate deposit-feeder or also a suspension-feeder. Gilbert (1977) gives a thorough account of the functional morphology of feeding and concludes that *M. balthica* is adapted to deposit-feeding but not to suspension-feeding. Others observed the inhalant siphon pointing vertically upwards and concluded that suspension-feeding is a second mode (i.e. Brafield and Newell, 1961; Rasmussen, 1973). However, an erect siphon does not necessarily imply suspension-feeding. An incurrent of overlying water may be primarily for respiration or for rinsing. On the experimental site, I observed *M. balthica* deposit-feeding, sometimes even probing the siphon into the sediment. Only occasionally did a siphon point upwards.

Competitive displacement

Field experiments where 1 species is added to the natural assemblage are usually designed to test the effects of competition. In the present case, the tube-dwelling polychaete *Pygospio elegans* abandoned the aggregates of both bivalves, *Macoma balthica* and *Cerastoderma edule*. This spionid polychaete feeds on small surface deposits as well as on suspended parti-

Table 2. Species composition and abundance (individuals. 12 cm⁻²) of Turbellaria in the absence of and within aggregates of *Macoma balthica*. D = diatom-feeder, B = bacteria-feeder, P = predator

No <i>Macoma</i>			Depth interval (cm)	With <i>Macoma</i>							
2	1	0		0	1	2	3	4	5	6	7
8	2	1		1	2	3	4	5	6	7	8
		1	D	<i>Postmecynostomum pictum</i> Dörjes	2						
		3	D	<i>Aphanostoma album</i> Dörjes							
		1	D	<i>Pseudaphanostoma pelophilum</i> Dörjes							
1	21		D	<i>Macrostromum pusillum</i> Ax	46						
		1	D	<i>Archimonotresis limophila</i> Meixner							
		2	D	<i>Provortex tubiferus</i> Luther	5						
		14	D	<i>Pogaina suecica</i> (Luther)	20	1					
		1	D	<i>Pogaina kinnei</i> Ax	1						
		3	B	<i>Philomecynostomum lapillum</i> Dörjes	4						
			B	<i>Retronectes brunea</i> n. n.							1
		8	B	<i>Bresslauilla relictata</i> Reisinger	3						
			B	<i>Balgetia semicirculifera</i> Karling					1		
		1	B	<i>Neoschizorhyn. parvorostro</i> Ax & Hell.	1	1	9	13	9	2	
				<i>Moevenbergia oculofagi</i> n. n.			1				
		1		<i>Rhinepera remanei</i> Meixner	1						
		2	P	<i>Paromalostomum dubium</i> (de Beauchamp)	2	1					
			P	<i>Haplopharynx rostratus</i> Meixner				1	1		
1	10		P	<i>Archilopsis unipunctata</i> (Fabricius)	17	5	7	5	13	6	1
			P	<i>Promonotus schultzei</i> Meixner	1						
			P	<i>Coelogyropora tenuis</i> Meixner				3	1		
			P	<i>Carenscoilia</i> spec.			1	1	3	2	
		1	P	<i>Polystyliphora filum</i> Ax		1	1		2		
			P	<i>Schizorhynchoides spirostylus</i> Boaden			1				
			P	<i>Cheliplanilla caudata</i> Meixner	1						
		2	P	<i>Cicerina brevicirrus</i> Meixner	6						
			P	<i>Typhlopolycystis</i> spec.				1			
		1	P	<i>Zonorhynchus seminascatus</i> Karling	1						
		2	P	<i>Placorhynchus octaculeatus</i> Karling							
		1	P	<i>Acorrhynchides robustus</i> Karling							
		1	P	<i>Halammovortex macropharynx</i> (Meixner)	1						
		3	P	<i>Proxenetes quinquespinosus</i> Ax	2						
			P	<i>Proxenetes quadrispinosus</i> Den Hartog	1						
		3	P	<i>Promesostoma caligulatum</i> Ax	2						
		6	P	<i>Promesostoma gracilis</i> Ax	8						
			P	<i>Promesostoma karlingi</i> Ehlers	1						
		4	P	<i>Promesostoma marmoratum</i> (Schultze)	15						
		2	P	<i>Promesostoma meixneri</i> Ax	1						
		7	P	<i>Promesostoma rostratum</i> Ax	13						
2	102			Sum of individuals	155	9	20	24	30	10	2
2	26			Sum of species	24	5	6	6	7	3	2

Table 3. Small Polychaeta in the absence of and within aggregates of *Macoma balthica*. Means (SD = standard deviation) of 6 samples of 2 cm²/0–8 cm. P = probability of error when assuming a difference; ns = P > 0.05 (Mann-Whitney U-test)

Individuals 2 cm ⁻² (SD)	No <i>Macoma</i>	With <i>Macoma</i>	U-Test P
All Polychaeta	14.3 (4.8)	19.7 (8.6)	ns
<i>Microphthalmus scelkowi</i> Meczniow	1.0 (1.5)	9.8 (7.9)	< 0.05
<i>Microphthalmus aberrans</i> (Webster & Ben.)	0.3 (0.5)	1.3 (1.5)	ns
<i>Spio filicornis</i> (O. F. Müller)	2.5 (3.3)	3.5 (1.6)	ns
<i>Pygospio elegans</i> Claparède	8.2 (4.6)	2.2 (1.9)	< 0.05
Others (6 ssp.)	2.3 (2.0)	2.9 (1.8)	ns
Species density	4.3 (1.6)	6.9 (0.9)	< 0.05
Species richness (12 cm ²)	10	9	

Table 4. Components of the turbellarian assemblage in the absence of and within aggregates of *Cerastoderma edule*. Means (SD = standard deviation) of 6 samples of 2 cm²/0-2 cm. There are no significant differences (Mann-Whitney U-test)

Individuals 2 cm ⁻² (SD)	No cockles	With cockles
All Turbellaria	21.0 (6.6)	21.5 (8.3)
Diatom-feeders (6 spp.)	10.3 (4.5)	10.2 (4.7)
Bacteria-feeders (5 spp.)	2.0 (2.1)	2.2 (1.8)
Predators (18 spp.)	8.7 (3.7)	9.2 (4.4)
Species density	9.2 (2.5)	9.3 (2.2)
Species richness (12 cm ²)	25	21

Table 5. Small Polychaeta in the absence of and within aggregates of *Cerastoderma edule*. Means (SD = standard deviation) of 6 samples of 2 cm²/0-2 cm. P = probability of error when assuming a difference; ns = P > 0.05 (Mann-Whitney U-test)

Individuals 2 cm ⁻² (SD)	No cockles	With cockles	U-test P
All Polychaeta	8.3 (3.2)	6.2 (3.2)	ns
<i>Microphthalmus szcelkowi</i>	0.7 (1.0)	2.7 (4.3)	ns
<i>Spio filicornis</i>	1.8 (1.9)	0.2 (0.4)	ns
<i>Pygospio elegans</i>	5.2 (1.5)	2.3 (1.6)	<0.05
Others (3 spp.)	0.7	0.8	ns
Species density	2.5 (1.2)	2.5 (0.8)	ns
Species richness (12 cm ²)	5	6	

cles (Hempel, 1957; Fauchald and Jumars, 1979). Thus there is an overlap with the food spectra of both bivalves. However, interference competition is more likely. Levin (1981, 1982) observed interference between spionid polychaetes (palp fighting) and I observed *P. elegans* to withdraw into its tube when touched by a siphon of *M. balthica*. Abundance of the related *Spio filicornis* was not affected by *M. balthica*, although it seems to feed in a similar way.

Exhalant siphons below surface

More conspicuous than this case of competition are the promotional effects of *Macoma balthica* on small fauna. High abundance of meiofauna in micro-oxic zones generated by macrofauna in the subsurface sediment are a general phenomenon, explained by the provision of oxygen and by an increased microbial activity serving as food to meiofauna (Aller and Yingst, 1978; Anderson and Meadows, 1979; Reise and Ax, 1979; Reise, 1981a, b).

Macoma balthica does not live in a burrow where overlying water is pumped downwards, as is the case with polychaetes. However, oxygenated zones can be

observed where siphons penetrate the sediment and also directly at the bivalves (Thamdrup, 1935; Ankar, 1977; this study). In thin aquaria, Ankar observed 'a water current finding its way from the exhalant siphon back along the inhalant siphon to the sediment surface'. In his drawing (Fig. 7 in Ankar, 1977), the exhalant siphon terminates within the reduced sediment layer. Probably the sediment around siphons is worked loose, allowing oxygenated water to spread from the exhalant siphon. This may be a side effect of mobility, but it also partly prevents the poisonous hydrogen sulfide of the sediment from direct contact with the tellinid.

Crucial for this effect seems to be that the exhalant siphon of *Macoma balthica* does not extend to the sediment surface. In the Tellinacea, exhalant siphons are usually shorter than the inhalant ones (Yonge, 1949) but there are few accounts detailed enough to distinguish between a siphon termination below or flush with the surface. *Tellina fabula* and *T. tenuis* are depicted by Salzwedel (1979) and Trevallion (1971) respectively, with the exhalant siphon lying horizontally within the sediment. Holme (1950), however, draws *T. tenuis* with the exhalant siphon extending to the surface. *M. nasuta* is reported to keep the exhalant siphon about 1 cm below surface (Hylleberg and Gallucci, 1975). Rasmussen (1973) and Gilbert (1977) show *M. balthica* with the aperture of the exhalant siphon flush with the surface. Ankar (1977) observed it to remain below surface, and so did I. Perhaps, this behaviour varies with sediment and locality, but more detailed observations are needed.

Nutrient enrichment

The termination of exhalant siphons below surface seems to be responsible for micro-oxic zones surrounding *Macoma balthica*. It will also produce localized concentrations of nutrients, notably nitrogen compounds. This will stimulate growth in microorganisms and diatoms. On sandy tidal flats where the experiment was done, Asmus (1982) measured nutrients and diatom growth and concluded that nitrogen compounds may be limiting to diatoms during summer. In July, ammonium and nitrate decreased down to zero. A siphon aperture flush with the surface, as in *Cerastoderma edule*, does not allow a localized effect under a tidal regime.

Colonization of subsurface sediment

Ankar (1977) observed abundant nauidids and nematodes close to siphons of *Macoma balthica*. In this

study, high abundance of Ciliata, Nematoda, Turbellaria and small Polychaeta is documented. The species composition suggests that the experimental *Macoma*-aggregates received their subsurface immigrants from the nearby burrows of the polychaete *Arenicola marina* (Reise and Ax, 1979; Reise, 1983). High numbers of the polychaete *Microphthalmus szelkowitzii* and the bacteria-feeding Turbellaria in the subsurface sediment within *Macoma*-aggregates imply an increased amount of food in form of microorganism. The strong predatory component in Turbellaria documents that a 3-level trophic web (microorganisms – grazers – predators) is maintained by *M. balthica* below the sediment surface.

Diatom-feeders at the surface

Macoma-aggregates not only increased the subsurface meiofauna but also those dwelling in the surface layer. Turbellaria in general and diatom-feeders in particular are significantly more abundant within aggregates than in controls. Woodin (1978) observed more small fauna in the shelter of tube-caps of the polychaete *Diopatra cuprea* and interpreted this as a refuge from epibenthic predation. Other examples of high abundance are explained as responses to biotic disturbances in the form of feeding funnels, fecal mounds and diggings (Thistle, 1980; Reise, 1981b; VanBlaricom, 1982) or to biotically mediated sediment stability (Rhoads and Young, 1971).

None of these examples seems to explain high abundance of diatom-feeding Turbellaria within aggregates of *Macoma balthica*. I suppose that part of the nutrients released by the tellinid below the surface become available to the diatoms above. In addition, the high biological activity encouraged by *M. balthica* in the subsurface is likely to provide the surface layer with even more nutrients. In the cockle aggregates, where exhalant siphons discharge directly into the overlying water, no positive response of diatom-feeding Turbellaria is observed.

Gardening

Where there is more food for diatom-feeding and bacteria-feeding meiofauna, there should be more food for *Macoma balthica* too. Both have bacteria and diatoms as a common food source, and predatory Turbellaria prey on Ciliata, Nematoda, Copepoda and others which in turn feed on bacteria and diatoms. Thus, the observed distribution of trophic guilds in Turbellaria suggests that *M. balthica* stimulates the growth of its own food source. This effect has been

termed 'gardening' in marine benthos and examples are feeding pockets of *Abarenicola pacifica* (Hyllberg, 1975) and mucus threads in nematodes (Riemann and Schrage, 1978; Warwick, 1981). In microcosms, Tenore and Rice (1980) added ciliates and meiofauna to deposit-feeding polychaetes. This not only enhanced mineralization but the polychaetes also increased their net incorporation rate of detritus. At moderate densities in microcosms, the mud snail *Ilyanassa obsoleta* stimulated diatom growth, possibly by accelerating nitrogen cycling (Connor et al., 1982). Newell (1965) cultured faeces of *Hydrobia ulvae* and *M. balthica* and observed a rapid increase of the nitrogen content, attributed to bacterial growth on a favourable substrate.

Using Turbellaria and small Polychaeta as bio-indicators, the present results demonstrate that *Macoma balthica* enriches the sediment with nutrients and thus cultures its own food source. Gerlach (1978) proposed that such 'gardening' is highly important in marine sediments.

The density of *Macoma balthica* in the experimental aggregates (1 individual 3 cm⁻²) which produced this 'gardening' effect is not an unrealistic one. In the Bay of Fundy, Tunnicliffe and Risk (1977) found 1 ind. 2.8 cm⁻². In Britain, Fraser (1932) records 1 ind. 1.7 cm⁻². At the experimental site, I found no more than 3 individuals below 1000 cm², however, on adjacent flats in earlier years I recorded much higher densities (Reise, 1978; own unpubl. data). Beukema et al. (1977) found that highest growth rates coincide with highest density in *M. balthica*. A result to be expected under the hypothesis of 'gardening'.

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