

ORIGINAL ARTICLE

Effects of the suspension feeding mussel *Mytilus trossulus* on a brackish water macroalgal and associated invertebrate community

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Conflicts of interest

The authors declare no conflicts of interest.

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Abstract

The importance of suspension-feeding mussels is particularly apparent in benthic communities; however, the role of this feeding strategy on the development of macroalgal and associated invertebrate communities is in general poorly known. The effect of suspension-feeding mussels *Mytilus trossulus* on benthic communities was studied in an *in situ* factorial field experiment in the Northern Baltic Sea over one ice-free season. The experiment was performed under different regimes of wave exposure (low and moderate) and on different sedimentary habitats (soft bottom with high organic content, soft bottom with low organic content, and hard bottom). In general the presence of mussels was associated with increased biomass of filamentous algae, herbivores and deposit feeders and decreased biomass of charophytes. The effect of *M. trossulus* interacted with the effect of exposure and substrate. Stronger responses were observed in moderately exposed than in sheltered areas. The presence of *M. trossulus* affected charophytes and deposit feeders on sand with low content of organic matter and filamentous algae on pebbles but not on other substrate types. The magnitude of the effects varied between months. The results suggest that (i) even in dynamic coastal systems the biodeposits and excretions of mussels are at least partly assimilated locally and are not flushed away to the open sea, (ii) the accumulation of faecal material induced elevated growth of deposit feeders, (iii) mussels enhanced the growth of ephemeral macroalgae and reduced the growth of perennial macroalgae, and (iv) together with increasing benthic primary production, mussels indirectly increase the production of herbivores.

Problem

Suspension-feeding mussels link water column productivity to the benthos by removing pelagic organisms, increasing rates of particle deposition and promoting nutrient recycling (Cloern 1982; Kotta & Møhlenberg 2002; Lauringson *et al.* 2007). Part of the deposited faeces and pseudofaeces are consumed by deposit feeders (Zhou *et al.* 2006) and the remaining part decomposes, thereby

increasing the availability of inorganic nutrients that may be channelled into benthic and pelagic production (Reusch *et al.* 1994; Marinelli & Williams 2003; Giles & Pilditch 2006). Besides notable biodeposition, bivalves excrete ammonia and thus may directly influence nutrient levels in seawater (Dame *et al.* 1991; Bracken 2004; Bracken & Nielsen 2004). Despite the importance of studies quantifying the effects of suspension feeders on macroalgal and associated invertebrate communities, such studies are

scarce (Reusch *et al.* 1994; Peterson & Heck 1999; Cummings *et al.* 2001) and often based on modelling approaches (*e.g.* Fulton *et al.* 2004; Dowd 2005).

It is generally known that increased sedimentation of organic matter leads to an increase in benthic algal production (Nilsson *et al.* 1991). It has been experimentally demonstrated that benthic algae take advantage of sediment nutrients through diagenesis (Cerco & Seitzinger 1997) as the algae can readily assimilate nutrients diffusing across the sediment surface (Asmus 1986). Consequently, macroalgae inhabiting sediments that are rich in organic matter can take advantage of remineralization and use porewater nutrients in periods of low nutrient levels in seawater. Thus, the growth of macroalgae is expected to be higher on sediments rich in organic matter than on sediments poor in organic matter. The presence of benthic suspension feeders may alter this relationship, as they are expected to reduce this nutrient limitation through considerable excretion of ammonia and biodeposition of organic matter and thereby increase algal growth.

The rate of biodeposition is dependent upon mussel density and availability of food (*e.g.* phytoplankton; Dame & Dankers 1988). The availability of food in turn depends on the concentration of phytoplankton and exchange of water. It is known that mussels can deplete the overlying water of algae (Fréchette *et al.* 1989; Peterson & Black 1991; Muschenheim & Newell 1992) and thus, food limitation may occur. Under food limitation, rising flow velocity (exposure) to a certain threshold value increases food supply and biodeposition rates. The added biodeposits, if not flushed away, may support the development of macrophytes and associated invertebrates. However, if mussels are not food limited then the mutualistic effects of mussels on adjacent biota are expected to be stronger in sheltered areas where the transport of biodeposits to deeper sea is lower than in exposed areas.

To date, strong links between suspension feeders, deposit feeders and macrophytes have been demonstrated in dense mussel beds, for example in the context of mussel farms and harvesting (Valentine & Heck 1993; Peterson & Heck 1999; Bologna & Heck 2002; Crawford *et al.* 2003; Airolidi *et al.* 2005). There exist a few *in situ* studies on evenly dispersed and less dense populations of suspension feeders (Norkko *et al.* 2001; Kotta *et al.* 2005), although such communities are widespread and typical of the coastal sea of South Africa, Baltic, Arctic and Antarctic Seas, to name just a few (Gutt 2001; Bownes & McQuaid 2006; Kotta *et al.* 2008). It is expected that the response of adjacent biota to the presence of suspension feeders is context-dependent. At high mussel densities notable biodeposition may deplete oxygen and result in hypoxic conditions, dominance of ephemeral algae and

opportunistic invertebrates. At low densities, however, the addition of mussels through a moderate fertilizing effect may foster the diversity of macrophyte assemblages and associated invertebrates (Bracken & Nielsen 2004).

In this study we experimentally evaluated the effect of the suspension-feeding mussel *Mytilus trossulus* Gould on macroalgal and associated invertebrate communities that occur in sediments differing in organic content and presence of rock and at different exposure regimes in the Northern Baltic Sea during one ice-free season. Our hypotheses were as follows:

- 1 Mussels enhance the growth of macrovegetation and increase the biomass of herbivores and deposit-feeders.
- 2 Increasing the degree of exposure may either amplify or weaken the effects.
- 3 The effects are stronger on organisms that occur in sediments poor in organic matter than on sediments rich in organic matter.

Study Area

The effects of the suspension feeder *Mytilus trossulus* on macroalgal communities and associated invertebrates were experimentally studied in Kõiguste Bay (58°22.10' N 22°58.69' E) in the Northern Baltic Sea during June–September 2004. The study area receives fresh water from a huge drainage area and therefore has reduced salinity of 5.0–6.5 psu. In general, the bottom relief of the area is quite flat, sloping gently towards deeper areas. The prevailing substrate types of the bay are sandy clay mixed with pebbles, gravel or boulders. The bottom depths of Kõiguste Bay are typically between 1 and 4 m. The area is moderately eutrophied (Kotta *et al.* 2008). The benthic vegetation is well developed and extensive proliferation of ephemeral macroalgae has been reported in the area in recent years. At the later stages of annual succession the drift algal mats may form in shallow areas and these mats provide macroalgae and invertebrates additional nutrient source (Lauringson & Kotta 2006). *Mytilus trossulus* dominates among suspension feeders with abundances and biomasses at 500 ind·m⁻² and 40 g dw·m⁻², respectively. The species inhabits hard substrata, but after establishing byssal connections among mussels, individuals may also form dense clumps in sedimentary habitats. As a result of the low salinity, mussel growth is reduced compared to fully marine areas and mussel length therefore rarely exceeds 2 cm (Kotta & Møhlenberg 2002).

Material and Methods

The experiment ran for 118 days from 3 June to 28 September 2004. The following factors and levels were included in the experimental design: exposure (sheltered

or moderately exposed site), mussels (presence or absence of *Mytilus trossulus*) and substrate (soft bottom with high organic content, soft bottom with low organic content, hard bottom). Each treatment was replicated three times. Experimental design included 144 plastic buckets (11 cm diameter, 10 cm deep) that were placed on the sea floor with the tops open.

Sand was extracted from nearby sea floor at eutrophied and clean sites representing soft bottom with high and low organic content, respectively. Prior to the experiment the sediment was sieved through a 1-mm mesh and dried in the sun for several days to ensure that it was free of living benthic invertebrates. To obtain similar starting conditions, sediment was homogenized before use. After homogenization, soft bottom with high and low organic content contained 0.025 and 0.008 % of organic matter, respectively. The buckets were filled up with sand and were seeded with three 10-cm-long shoots of *Chara aspera* Willdenow cut from plants shortly after sampling. This charophyte species is a dominant member of the phytobenthos in the shallower parts of the study area. Other buckets were filled with pebbles (average diameter 7 cm) that were large enough to be retained in the bucket. The pebbles were collected from the seashore and were devoid of vegetation.

Mytilus trossulus were collected from Kõiguste Bay. The experimental individuals were similar in size at the beginning of the experiment. The average length of *M. trossulus* deployed in the experiment was 15 mm. Three individuals of *M. trossulus* were added to each bucket corresponding to a density of 315 ind·m⁻² which is comparable to natural densities at Kõiguste Bay (Lauringson & Kotta 2006; Kotta *et al.* 2008).

The buckets were placed on the sea floor at 1.5 m depth. Half of the buckets were placed in the sheltered and another half in the moderately exposed part of the bay. Simplified Wave Model method was used to calculate the wave exposure for mean wind conditions represented by the 10-year period between 1 January 1997 and 31 December 2006 (Isæus 2004). A nested-grids technique was used to ensure long-distance effects on the local wave exposure regime, and the resulting grids had a resolution of 25 m. The borderline between low and moderate exposure was set at 100,000. At both sites current velocity was measured at 1-s intervals using a calibrated electromagnetic current recorder connected to a data logger (Compact-EM data recorder by Alec Electronics). This instrument also records data on water temperature. The flows were significantly different between exposed and sheltered areas ($3 \pm \text{SE } 2 \text{ cm} \cdot \text{s}^{-1}$ in the sheltered area and $11 \pm \text{SE } 3 \text{ cm} \cdot \text{s}^{-1}$ in the moderately exposed area). Temperature did not vary between the two sites and was estimated at 15 °C in June and September and 20 °C in July and August.

The buckets were sampled monthly from June to September. All bucket contents were sieved through a 0.25-mm mesh and placed into plastic bags and frozen prior to laboratory analysis. In the laboratory all samples were sorted under a binocular microscope (20–40× magnification). All individuals were identified to the species level except for oligochaetes, chironomids, and juveniles of gammarid amphipods. Individuals of all taxa were weighed. Prior to weighing, animals and plants were dried at 60 °C for 2 weeks.

The effects of mussels, exposure and substrate on the biomass of seeded and recolonized macroalgal and invertebrate groups were assessed by a repeated measures factorial ANOVA. Using a standard ANOVA in our case is not appropriate because it fails to account for the correlation between the repeated measures, and the data therefore violate the ANOVA assumption of independence. Post-hoc Bonferroni test was used to determine which treatment levels were statistically different from each other in different months (StatSoft, Inc. 2007).

Results

In the absence of *Mytilus trossulus* the biomass of filamentous algae was highest in June and declined thereafter. The biomass of charophytes was relatively stable over the course of the experiment. Substratum composition affected the dominance structure of filamentous algae. Pebbles were characterized by higher biomasses of *Ulva intestinalis* L. and *Pilayella littoralis* (L.) Kjellman compared to other substrate types. Exposure affected the biomass level of charophytes, with higher biomass associated with the moderately exposed area (Fig. 1).

The biomass of herbivores increased over the course of experiment. Substrate type had consistent effects on herbivores. The biomass of gammarid amphipods, *Theodoxus fluviatilis* (L.) and *Hydrobia ulvae* (Pennant) was significantly higher on pebbles compared to sediments with low and high content of organic matter. The biomass of deposit feeders also increased significantly over time but the changes were less marked. Substrate type had consistent effects on deposit feeders. The biomass of *Macoma balthica* (L.) and Chironomidae larvae was highest in hard bottoms, intermediate in soft bottoms with high content of organic matter, and lowest in soft bottoms with low content of organic matter (Fig. 2).

The repeated measures ANOVA analyses indicated mostly consistent community responses to the experimental treatments. The presence of *M. trossulus* had significant effects on filamentous algae, charophytes, herbivores and deposit feeders. The direction of the effect varied among months and organism groups. The presence of *M. trossulus* resulted in elevated biomasses of filamentous algae and

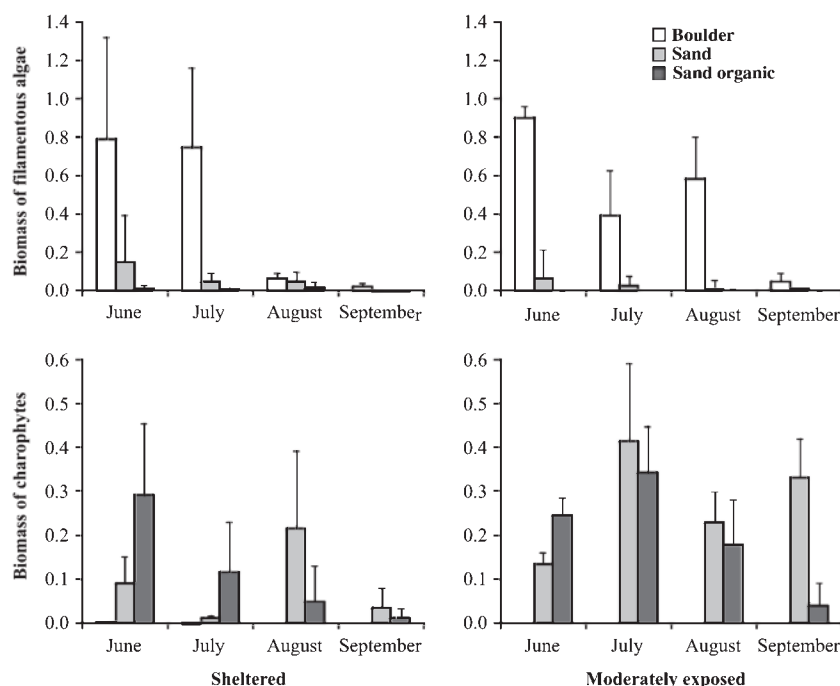


Fig. 1. Seasonal changes in the biomass of filamentous algae and charophytes (g dry weight, mean per bucket \pm SD, N = 3) at different substrate and exposure levels in the absence of *Mytilus trossulus*.

deposit feeders at the initial stages of algal succession (June, July) and in diminished biomass of charophytes at the later stages of algal succession (August, September). The positive effect of *M. trossulus* on herbivores was significant from July to September (Table 1, Fig. 3).

The interactive effect of *M. trossulus* and exposure was only significant for macroalgae and not for benthic inverte-

brates. Stronger responses in macroalgal growth were observed in moderately exposed than in sheltered areas. The direction and timing of responses corresponded to the separate effect of *M. trossulus* on the respective organisms (Fig. 4).

Interactions between substratum and *M. trossulus* were significant for all organism groups except herbivores. The

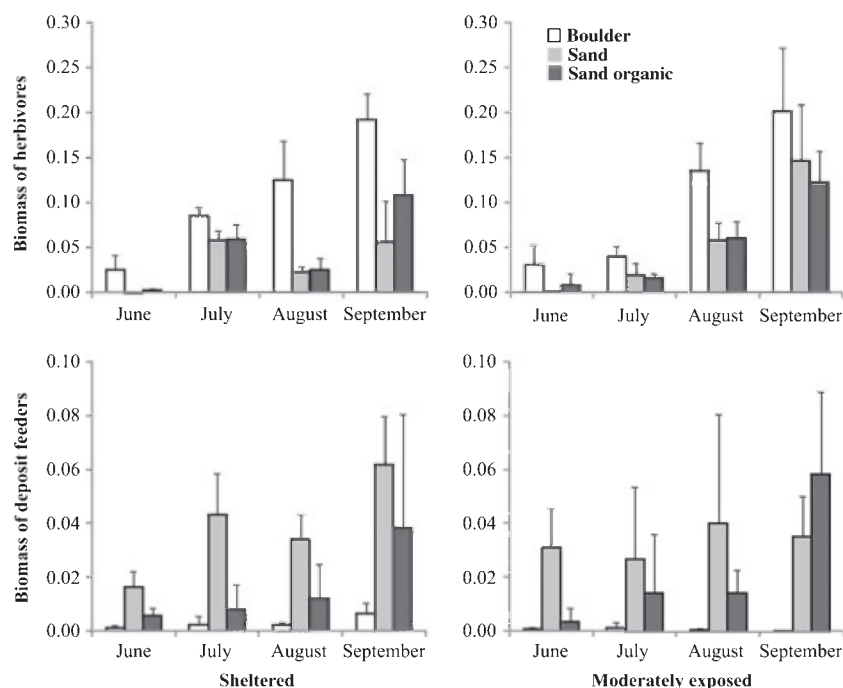


Fig. 2. Seasonal changes in the biomass of herbivores and deposit feeders (g dry weight, mean per bucket \pm SD, N = 3) at different substrate and exposure levels in the absence of *Mytilus trossulus*.

Table 1. Repeated measures factorial ANOVA analyses on the separate and combined effects of *Mytilus trossulus*, exposure and substrate type on filamentous algae, charophytes, herbivores and deposit feeders. n.s. refers to non-significant effect and × stands for interaction.

Model/Factor	F	Effect df	Error df	P
Filamentous algae				
Exposure	4.40	4	21	0.010
<i>Mytilus</i>	3.94	4	21	0.015
Substrate	16.79	8	42	0.000
Exposure × <i>Mytilus</i>	12.94	4	21	0.000
Exposure × Substrate	3.60	8	42	0.003
<i>Mytilus</i> × Substrate	2.29	8	42	0.040
Exposure × <i>Mytilus</i> × Substrate	8.50	8	42	0.000
Charophytes				
Exposure	12.19	4	13	0.000
<i>Mytilus</i>	5.73	4	13	0.007
Substrate	13.63	4	13	0.000
Exposure × <i>Mytilus</i>	3.76	4	13	0.030
Exposure × Substrate	2.41	4	13	n.s.
<i>Mytilus</i> × Substrate	7.30	4	13	0.003
Exposure × <i>Mytilus</i> × Substrate	5.22	4	13	0.010
Herbivores				
Exposure	7.77	4	21	0.001
<i>Mytilus</i>	3.21	4	21	0.033
Substrate	6.45	8	42	0.000
Exposure × <i>Mytilus</i>	0.62	4	21	n.s.
Exposure × Substrate	0.85	8	42	n.s.
<i>Mytilus</i> × Substrate	1.08	8	42	n.s.
Exposure × <i>Mytilus</i> × Substrate	0.63	8	42	n.s.
Deposit feeders				
Exposure	1.93	4	21	n.s.
<i>Mytilus</i>	6.07	4	21	0.002
Substrate	26.70	8	42	0.000
Exposure × <i>Mytilus</i>	2.33	4	21	n.s.
Exposure × Substrate	2.15	8	42	n.s.
<i>Mytilus</i> × Substrate	3.25	8	42	0.006
Exposure × <i>Mytilus</i> × Substrate	1.17	8	42	n.s.

presence of *M. trossulus* increased the biomass of deposit feeders and decreased the biomass of charophytes on sand with low content of organic matter but not on other substrate types. The presence of *M. trossulus* also resulted in the elevated biomass of filamentous algae on pebbles but not on sandy substrate. There were no differences in timing of the combined and separate effects of mussels (Fig. 5).

Discussion

Our study showed that the presence of mussels was associated with an increase in the biomass of ephemeral macroalgae (hypothesis 1). This increase suggests that mussels provide an important local-scale nutrient source for macroalgae inhabiting the shallow water benthic ecosystems

of the Baltic Sea. The provisioning of additional habitat (shells for attachment) was not considered a viable explanation due to their small sizes (1.5–2 cm) and lack of epiphytes on bivalves at the end of the experiment.

The addition of nutrients may be either direct (through nitrogenous excretory products) or indirect (through biodeposition and subsequent remineralization) (Kautsky & Wallentinus 1980; Dame *et al.* 1991; Bracken & Nielsen 2004; Kotta *et al.* 2006a). It has been shown earlier that nitrogen and organic content is higher in biodeposits than in naturally sedimenting material (Kautsky & Evans 1987). In either scenario it is surprising that even a few mussels can significantly modify soft- and hard-bottom habitats in this dynamic ecosystem.

The mussels significantly increased macroalgal growth at the initial stage of annual succession. It is plausible that *Mytilus trossulus* accelerates the growth of macroalgae through the entire productive season. However, at the later stages of annual succession the effect is likely counteracted by heavy grazing pressure by mesoherbivores. This hypothesis is supported by a significantly higher biomass of grazers in *M. trossulus* treatments in August and September compared to other treatments.

The biomasses of aquatic plants and mesoherbivores are positively correlated in many water bodies as plants provide mesoherbivores with habitat and food resources (Huntly 1991; Lawton 1994; Kotta & Orav 2001; Orav-Kotta & Kotta 2004). Animals respond more strongly to the amount of available resource than to the diversity of plants that provide it (Parker *et al.* 2001; Kotta *et al.* 2006b) and this assertion may explain the consistent effect of *M. trossulus* on herbivores (hypothesis 1), especially on gammarid amphipods, even though the macroalgal assemblages varied among buckets. In our study area gammarid amphipods are capable of foraging different types of food; however, when the filamentous brown alga *P. littoralis* is present it seems to be the most important dietary component of the studied gammarids (Orav-Kotta *et al.* 2009). In the current study *M. trossulus* consistently enhanced the growth of *Pilayella littoralis* over other macrophyte species and this may explain the stronger response of gammarid amphipods compared to other herbivores.

Deposit feeders are often food limited in the temperate coastal marine ecosystems (Levinton & Stewart 1988; Ólafsson & Elmgren 1997; Kotta *et al.* 2001). As seen in the present study, biodeposition by suspension-feeding mussels may reduce or even release deposit feeders from food limitation (hypothesis 1). Our results agree with earlier circumstantial and experimental evidence that the accumulation of faecal material induces elevated settlement and growth of deposit feeders (Posey 1986; Dittmann 1990; Snelgrove & Butman 1994). Strong effects of

Fig. 3. Seasonal changes in the separate effects of *Mytilus trossulus* on the biomasses of filamentous algae, charophytes, herbivores and deposit feeders (g dry weight, mean per bucket \pm SD, N = 18).

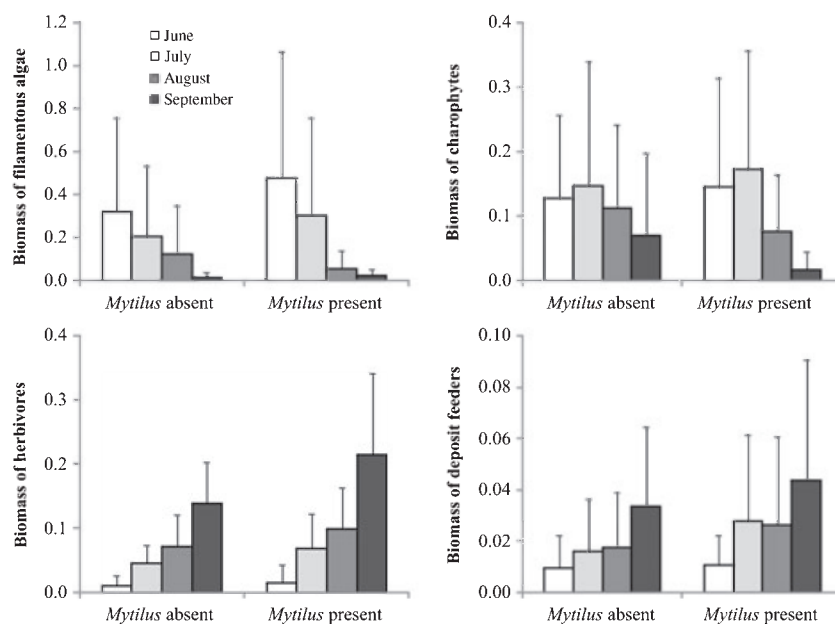
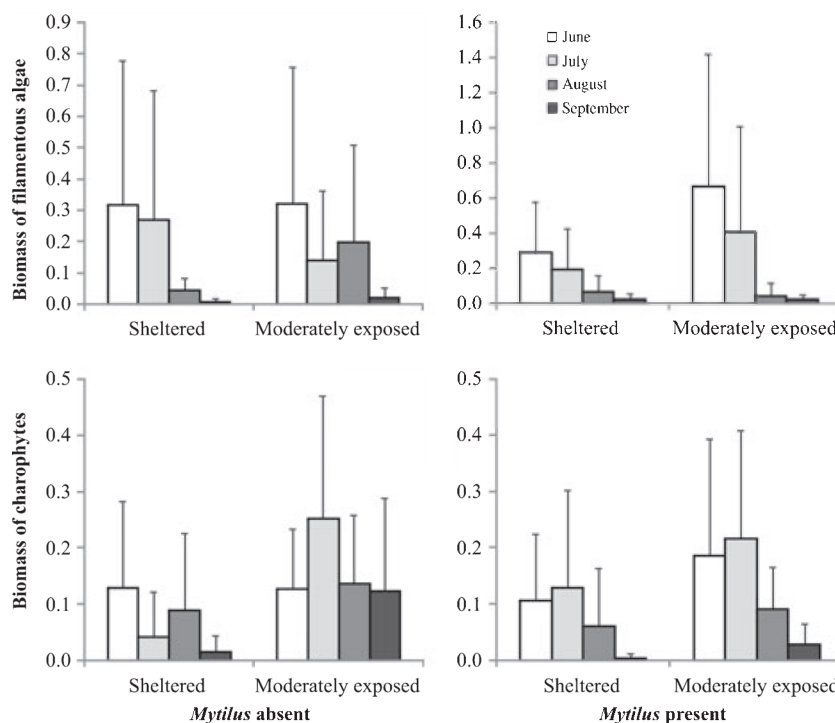


Fig. 4. Seasonal changes in the combined effects of *Mytilus trossulus* and exposure on the biomasses of filamentous algae and charophytes (g dry weight, mean per bucket \pm SD, N = 9).



mussels on deposit feeders were observed in the early stages of annual succession. At the later stages of annual succession, drift algae and their decomposition products provide an additional source of fresh detritus for deposit feeders (Kotta *et al.* 2008) and may explain weak effects of mussels in this period.

The interaction of exposure and *M. trossulus* affected the biomass structure of filamentous algae (hypothesis 2).

Except for phytoplankton blooms, the suspension-feeding bivalves are often limited by the availability of suspended particulate matter (Incze *et al.* 1981; Fréchette *et al.* 1989; Smaal *et al.* 2001) and increasing current velocity can reduce this limitation (Walne 1972; Fréchette & Bourget 1985; Wildish *et al.* 1992). Our study demonstrated that suspension-feeding mussels had stronger positive effects on filamentous algae in moderately exposed areas than in

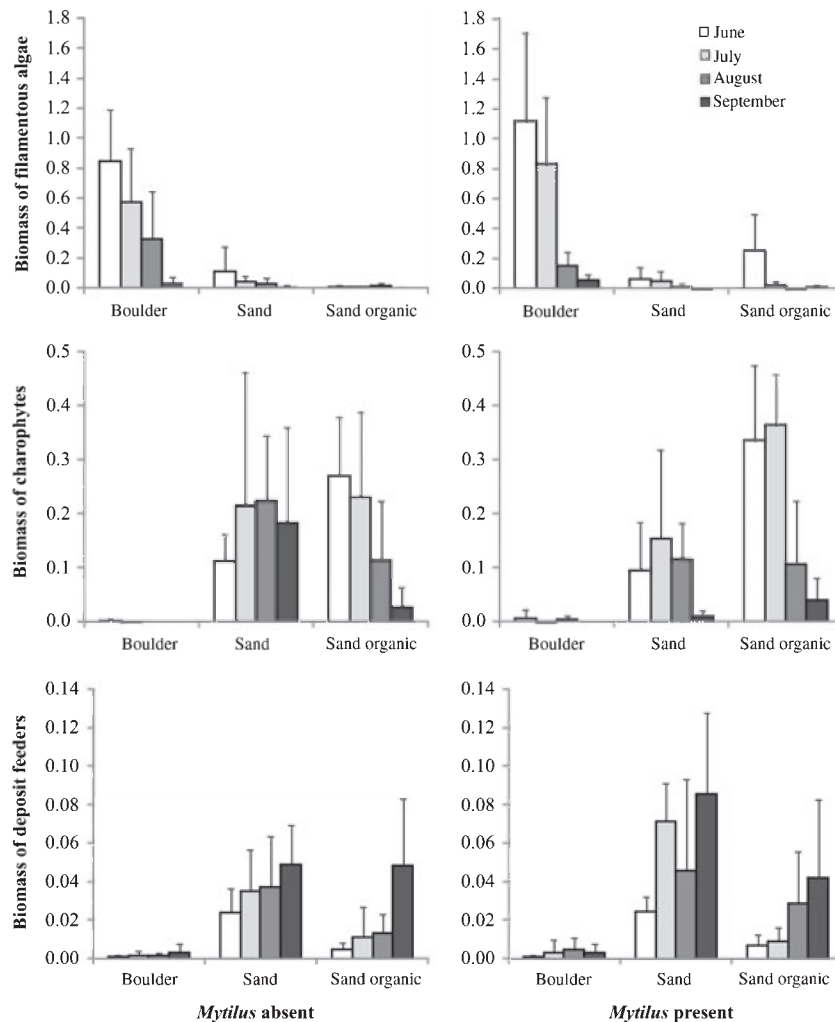


Fig. 5. Seasonal changes in the combined effects of *Mytilus trossulus* and substrate type on the biomasses of filamentous algae, charophytes and deposit feeders (g dry weight, mean per bucket \pm SD, N = 6).

sheltered areas. This difference suggests that mussels were food limited because biodeposition activity was higher in exposed areas with high food availability compared to sheltered sites with low food availability (Kotta *et al.* 2005).

We predicted that the effect of *M. trossulus* would be stronger on sediments poor in organic matter compared to sediments rich in organic matter (hypothesis 3). A significant combined effect of substrate and *M. trossulus* was observed only for deposit feeders. Besides, the presence of *M. trossulus* decreased the growth of charophytes inhabiting sand with low content of organic matter, whereas such an effect was not observed on other substrate types. The apparent lack of interactive effect of substrate and mussels on macroalgae indicates that sediment nutrients were generally not available to algae, and factors, *e.g.* those affecting remineralization and the diffusion, advective

tion or turbulent mixing of porewater nutrients, limited the transport of sediment nutrients to the water column.

The presence of mussels resulted in the decline of charophytes at the later stages of annual succession. As shown earlier, mussels increase nutrient loads, leading to elevated productivity of ephemeral macroalgae. When covered by filamentous algae, charophyte photosynthetic activity presumably decreases and the charophytes become very attractive to herbivores (Kotta *et al.* 2004). Heavy grazing pressure on charophytes is expected given that there was significantly higher grazer biomass in *M. trossulus* treatments.

To conclude, our experiment demonstrated that *M. trossulus* had significant effects on macroalgae and associated invertebrates, especially during early stages of annual succession. Although benthic communities in the Baltic Sea are considered to be primarily physically

controlled (e.g. Herkül *et al.* 2006), our study indicates that physical and biological factors interactively affect benthic community composition at small spatial scales.

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