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Habitat structure and complexity as determinants of biodiversity in blue mussel beds on sublittoral rocky shores

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Abstract Habitat-forming, ecosystem engineer species are common in most marine systems. Still, much uncertainty exists about how individual and population-level traits of these species contribute to ecosystem processes and how engineering species jointly affect biodiversity. In this manipulative field experiment, we examined how biodiversity in marginal blue mussel beds is affected by blue mussel (1) body size, density and patch context and (2) presence of fucoid and algal structures. In the study area, bladder-wrack (*Fucus vesiculosus*), filamentous algae and blue mussels (*Mytilus edulis*) coexist at shallow depths in a variety of patch configurations and offer complex habitats with a high variability of resources. We hypothesized that complexity in terms of mussel bed structure and algal presence determines species composition and abundance. Results from the experiment were compared with macrofaunal communities found in natural populations of both engineering species. Results show that the physical structure and blue mussel patch context are important determinants for species composition and abundance. Results further show that the presence of algal structures positively affects diversity in blue mussel habitats due to increased surface availability and complexity that these algae offer. This study shows that blue mussel beds at the very margin of their distribution have an indisputable function for promoting and maintaining biodiversity and suggest that facilitative effects of habitat-modifying species are important on Baltic Sea rocky shores with fundamental importance to community structure.

Introduction

Ecosystem engineering by organisms plays a major role in determining the structure and functioning of most ecosystems, yet the underlying mechanisms are not well understood (Bruno and Kennedy 2000; Lilley and Schiel 2006). Ecosystem engineer species are organisms that modulate the availability of resources causing changes in the physical state of biotic or abiotic materials. Through their activities they modify, maintain and create habitats facilitating the existence of other species (Jones et al. 1994). Ecosystem engineers may add new species to an ecosystem increasing species diversity and/or influence the performance and abundance of species able to inhabit both engineered and unmodified patches (Badano and Marquet 2008). The engineering roles of species may become especially important in species boundary areas since density, population structure and dynamics differ from core areas (Gaston 2003; Travis 2004). In light of increasing rates of extinction, the task of determining how diversity is linked to changes in the abundance of ecosystem engineer species is becoming ever more pressing.

In the shallow non-tidal northern Baltic Sea, blue mussels *Mytilus edulis* L. and the fucoid *Fucus vesiculosus* L. (hereafter *Fucus*) coexist in large beds or as mosaics of

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various sized patches (Westerbom et al. 2002; Wikström and Kautsky 2007). Both are globally known to function as ecosystem engineers (e.g. Kautsky et al. 1992; Crooks and Khim 1999). They uphold rich faunal communities in a number of ways: by creating habitats (e.g. Suchanek 1980; Wikström and Kautsky 2007), by altering sediment fluxes (Commito et al. 2005), by modifying nutrient content (Kautsky and Wallentinus 1980; Norling and Kautsky 2007) and by offering food (Kautsky and Wallentinus 1980; Kangas et al. 1982) and hideouts from predators (Tsuchiya and Nishihira 1985; Duffy and Hay 1991). The positive effects of ecosystem engineers can be conditioned by their individual properties, for example age, size and physical structure or at larger scales by patch structure and density (e.g. Gee and Warwick 1994; Jelbart et al. 2006; Palomo et al. 2007). Most investigations into biogenic habitat provision consider the promotion of local biodiversity by single species, yet habitat-forming species are often themselves components of diverse assemblages and shaped by multiple, co-dominating engineering species like forests, mussel beds and algal canopies (e.g. Miyamoto and Noda 2004; Mori and Komiyama 2008). While this is recognized by modern theory (Bruno and Bertness 2000; Stachowicz 2001; Wright and Jones 2006), only few attempts to evaluate the possible functional and structural differences between single and multiple facilitators and their interactions exist (Chapman et al. 2005; Yakovis et al. 2008). Coexisting engineers, especially those from one guild (sensu Root 1967), may promote similar faunal communities and even compensate for each other (Kraufvelin and Salovius 2004). However, if the faunal communities hosted by two co-occurring ecosystem engineers markedly differ from each other, the loss of one species may radically lower biodiversity and resilience having severe impacts on the entire ecosystem.

In the study area, *Fucus* and blue mussels exist at the edge of their range ultimately set by low salinity conditions. Biomass and coverage of these species therefore vary in time and space with possible effects on the abundance and composition of associated organisms (Kangas et al. 1982; Kiirikki 1996a; Råberg and Kautsky 2007; Wikström and Kautsky 2007). Predicted declines in sea water salinity caused by climate change (Omstedt and Hansson 2006) could markedly alter the structure and coverage of these engineering species or even cause their disappearance from the northern Baltic Sea (e.g. Kiirikki and Ruuskanen 2000; Westerbom et al. 2002). Although *Fucus* and blue mussel communities have been extensively studied elsewhere, very little is known about the interaction between the two species and their additive effects on community structure on sublittoral shores. In the study area, *Fucus* is virtually never found without blue mussels, and blue mussels are generally the most dominant species in *Fucus* stands (e.g. Kangas et al. 1982; Kautsky et al. 1992; Wikström and Kautsky 2007). Classical models explaining species diversity patterns predict a positive relationship between habitat complexity and species diversity (Bazzaz 1975; Pianka 1988) but empirical results are often contradictory, especially in marine habitats (Kelaher 2003; Cole 2009). In the Baltic Sea, very little attention has been given to the mechanisms that drive macrobenthic assemblage development in relation to habitat complexity (see however Råberg and Kautsky 2007) and apart from sandy bottoms, no attempts have been made to experimentally demonstrate the role of blue mussels on benthic biodiversity on rocky shores that dominate coastal areas of the northern Baltic Sea. Understanding the drivers and consequences of site quality for a given system has important implications for metapopulation dynamics, conservation, resource management and restoration.

This study was planned to examine how the structure of blue mussel patches affects associated fauna in terms of species number, diversity and individual abundance. Specifically, we wanted to test how (1) the body size, mussel density and patch context and (2) presence of fucoid or algal structures in mussel beds affect macrofaunal biodiversity. We hypothesized that blue mussel patch structure affects the faunal communities and that *Fucus* and mussels, together by complementing each other, increase the overall diversity in mussel beds on Baltic rocky shores. Finally, we hypothesized that increased structural complexity alone affects species diversity and individual abundance in blue mussel beds.

Methods

Study site and experimental design

The study was carried out in the outer archipelago area of the non-tidal western Gulf of Finland (59°48′N, 23°12′E). This area contains a range of blue mussel habitat configurations, from large, continuous mussel beds to areas with a few small blue mussel patches surrounded by areas with low mussel coverage. Blue mussel beds show large interannual fluctuations in density and population structure due to salinity, ice scouring and predation (Westerbom et al. 2002).

In order to experimentally test the importance of blue mussel patch structure and to test if algal structures increase diversity in mussel beds, we cleared a 15 × 15 m^2 area originally characterized by mixed assemblages of mussels and *Fucus*. Eight different treatments (Table 1, $n = 10$ treatment^{-1}) consisting of the engineering species with controls were then created and placed in eight rows and ten columns with 1-m distance between treatments. Treatments were randomly allocated to cells within columns (each treatment

Table 1 The different patch characteristics used in the experimental setup

		Abbreviation	Patch size (cm)
1	Blue mussels of small size	SM	20 × 20
2	Blue mussels of mixed size	M	20 × 20
3	Small patch of blue mussels	SP	10 × 10
4	Blue mussels and artificial algae	AAM	20 × 20
5	Blue mussels and *Fucus*	FM	20 × 20
6	Artificial algae	AA	20 × 20
7	*Fucus*	F	20 × 20
8	Bare rock patches lacking mussels and *Fucus*	BR	20 × 20

All treatments containing mussels consisted of blue mussels of mixed size (0.8–3.5 cm) except for the SM treatments (0.8–1.5 cm). $N = 80$

occurring only once in each column), however, so that they were interspersed and any artifact of being placed on the edge of the grid was distributed among all treatments as best possible (each treatment occurring 4 times at the edge). This was done in order to reduce possible edge effects. The experimental area is located at a homogeneous natural sublittoral platform at ca 4.5 m depth with no irregular topographic features except for a slow increase in depth (depth differences among treatments: ANOVA, $F_{7,\ 72} = 0.46$, $P = 0.86$) and no other observable gradients running over the area. The entire experimental area was lined with a > 2 m wide buffer zone completely cleared of all benthic organisms and free of treatments to further reduce the effects of the surrounding environment.

Patches with differently sized mussels, “small mussels” (SM, 8–15 mm) and “mixed mussels” (M, 8–35 mm), were constructed to investigate if the body size of mussels affects the associated community. Small patches (SP; 10 × 10 cm instead of 20 × 20 cm that were used in all other treatments) were used to explore how mussel patch size and the surrounding mussel free context area affects the faunal communities (henceforth called small patch). These areas surrounding mussel patches in the study area are frequently covered with microfilms of diatoms and filamentous algae during summer months (Snoeijs and Kautsky 1989; Kiirikki and Lehvo 1997) with possible effects on the faunal communities (e.g. Kraufvelin and Salovius 2004). Patches with artificial algae and mussels (AAM) and *Fucus* and mussels (FM) were made to study if the presence of algal structures in blue mussel beds affects the biodiversity. These natural and artificial algae were not designed to perfectly match each other but to increase the three dimensional complexity of mussel beds and to separate effects of structure alone from both the structural and biological functions of algae. Patches with artificial algae (AA) and *Fucus* (F) were assembled to reveal the role of algal structures and to function as controls. Bare rock (BR) patches mimicked natural bottoms devoid of perennial structures, however, including annual filamentous structures that cover these shores during the summer season (Table 1). There were no significant differences between the mussel density between FM, AAM and M (ANOVA, $F_{2,\,27} = 1.018$, $P = 0.38$).

Transplanted blue mussels were collected by SCUBA after which mussels were separated with sieves and sorted by size into two size categories (SM and M). Mixed mussels were used in all treatments containing mussels except for the patches with small mussels (SM). All mussels were cleansed of epibiota. After collecting and separating mussels, 80 plastic, bottom- and roofless frames (20(b) × 20(l) × 10(h) cm, mesh size 5 mm) were attached to the bottom of the experimental area with the help of wedges previously drilled into the rock bottom in order to allow mussels to re-attach to the bedrock. Mussel biomass was kept constant between all mussel treatments of equal patch size (ANOVA, $F_{3,\,36} = 0.85$, $P = 0.44$). Also, *Fucus* was sampled and cleansed from organisms, and one individual (average DW 21.3 g ± 1.36 SE) was attached to treatments containing *Fucus*. The two treatments with *Fucus* had an equal algal biomass ($t_{18} = -1.476$, $P = 0.43$). Artificial algae equivalent to the frond height of *Fucus* were constructed using a rigid plastic rope and attached to the AA and AAM treatments. All artificial algae were 15 cm high. After placing mussels, *Fucus* and artificial algae within the frames in May 2007, the patches were left open for colonization for >4 months. To reduce cage effects, all frames were removed after 3 months, leaving behind only the 80 patches with engineering species. In September 2007, all experimental patches were sampled by scraping off the mussels using a 20 × 20 cm square frame with an attached net bag (see Westerbom et al. 2002; Råberg and Kautsky 2007). The small patches (SP) were sampled with the patch in the center, and the remaining mussel-free area within the frame was also scraped. The mussel biomass in patches at the start and end of the experiment corresponded to naturally occurring biomasses of mussels (1–4 g DW soft tissue patch^{-1}, Westerbom and Jattu 2006).

In addition to experimental treatments, samples from natural blue mussel beds were collected to test the hypothesis that the density of the mussel bed affects diversity ($N = 30$). Sampled patches were of similar size as experimental treatments and randomly chosen. Three density categories (sparse, intermediately dense and dense) were chosen by visually estimating the coverage percent of the blue mussels in patches. Naturally occurring *Fucus* patches ($N = 10$) were also sampled for a natural reference from *Fucus* patches equivalent to the experimental treatments. All patches were sampled using a 20 × 20 cm square frame and collected at 5 m depth.

Sampling and processing

The sampled fauna in all patches was separated by size through a series of sieves with the mesh sizes 9.5, 4, 2, 1 and 0.5 mm and all individuals were counted. The fauna was identified to nearest possible taxa. The smallest fraction in all samples was analyzed using a microscope. Barnacles *Balanus improvisus* Darwin and the bryozoa *Electra crustulenta* (Pallas) were excluded from the analysis in the experimental patches since these were already present as epiphytes on mussel shells at the beginning of the experiment and could not be removed without harming the mussels. Blue mussel biomass was calculated according to the formula presented in Westerbom et al. (2002).

Benthic functional groups

To investigate the functional role of the different species, each species was assigned to a functional subgroup according to Pearson and Rosenberg (1987). This system categorizes organisms based upon their mode of feeding, type of mobility and method of food capture. The diversity of functional traits in an ecosystem is considered more important than the diversity of its species, and the number of functional groups in an ecosystem can also reveal how different types of organisms are affected by the activity of a bioengineer (Castilla et al. 2004). Changes in functional variables may be more informative than the identification of static relationships between environmental variables and single species alone (Fonseca et al. 1990). This grouping system included five main trophic types—suspensivores, detrivores, herbivores, carnivores and parasites. Mobility categories included mobile, semi-mobile and sessile types. Finally, species were also categorized based on the method of food capture. This classification system resulted in ten different functional categories.

Statistical analyses

To explore sources of differences in invertebrate diversity, one-way ANOVAs were performed on total abundances of invertebrates (defined as total number of individuals regardless of species), on taxon richness and on numbers of functional groups. ANOVAs were followed by *a posteriori* Tukey tests to identify means that differed significantly at $\alpha = 0.05$. Since one single taxon (*Hydrobia* spp.) contributed strongly to individual density in all treatments, total abundance of individuals was also tested excluding this taxon. To study differences in invertebrate diversity in the natural mussel and *Fucus* patches, one-way ANOVAs were done on total abundances of invertebrates and on taxon richness. All community data met assumptions for parametric testing (normality tested with Wilk Shapiro, homogeneity of variance tested with Levene's test).

Spearman rank tests on non-normal data were carried out to test whether the filamentous algal and fucoid biomass in the experimental patches correlate with the number of species in the different patch types since a small amount of filamentous algae was present in treatments and might affect species diversity. Shannon index of diversity (H' based on log e) was calculated for the faunal communities in all patches using abundance as the unit. The correlation between blue mussel biomass and average species number in all treatments was tested with a Spearman rank test. All tests were carried out with SPSS 16.0.

To test whether the species composition and the abundance of functional groups in the different types of treatments differed, the treatment types were subjected to a non-metric multidimensional scaling (nMDS) ordination based on Bray–Curtis dissimilarity with the PRIMER-6 package (Clarke et al. 2006). The effect of treatment type was tested on all treatments using analysis of similarity (ANOSIM) based on Bray–Curtis dissimilarity on forth root (analysis of species composition) and log + 1 (analysis of functional groups) transformed data followed by the SIMPER procedure to determine taxa predominantly responsible for differences between the assemblages.

Results

Effects of patch structure on the communities

The experimental patch treatments showed marked differences regarding faunal composition. A total of 25 taxa were found, some species being entirely restricted to patches with blue mussels (*Fabricia stellaris* (O.F. Müller), *Mya arenaria* (L.)) or only occurring sparsely in other patches (*Hediste diversicolor* (O.F. Müller), *Marenzelleria viridis* (Verrill), Turbellaria, *Prostomatella obscura* (Schultze); Table 2). The number of species did not differ between treatments with the exception of the bare rock patches that harbored significantly fewer species than all other patches except the small patches (SP) and *Fucus* patches (F) (Fig. 1a; ANOVA, $F_{7,\ 72} = 2.97$, $P < 0.01$). Individual abundance differed significantly between treatments (Fig. 1b; ANOVA, $F_{7,\ 72} = 4.469$, $P \leq 0.001$): treatments with mussels of mixed size (M) and mussels and algal structures (FM, AAM) contained more individuals than small mussel patches (SP; 10 × 10 cm) and bare rock patches (BR). Patches with *Fucus* and mussels (FM) also had a higher individual abundance than patches with small mussels (SM) (Tukey, $P \leq 0.05$).

When *Hydrobia* spp. was left out from the analysis, differences in individual abundance were also significant (Fig. 1c; ANOVA, $F_{7,\ 72} = 23.064$, $P \leq 0.001$). The bare rock patches (BR), the patches with small mussels (SM)

Table 2 Average abundance of macrofauna (ind. 0.04 $m^2 \pm$ SE) in the experimental mussel patches and *Fucus* patches

Taxon	F	FM	M	AA	AAM	SP	SM	BR	*P*
Mollusca									
New Mytilus edulis	3.5 ± 0.9	7.1 ± 1.4	10.8 ± 1.0	4.0 ± 0.7	6.9 ± 0.7	4.6 ± 1.0	5.6 ± 0.7	6.0 ± 0.6	***
Cerastoderma glaucum	29.1 ± 6.5	37.9 ± 7.1	8.1 ± 4.8	53.1 ± 6.2	33.0 ± 3.9	37.7 ± 4.9	23.8 ± 4.2	43.6 ± 7.1	***
Macoma baltica	16.5 ± 4.4	9.0 ± 1.5	8.1 ± 1.5	32.9 ± 8.0	7.8 ± 2.7	17.1 ± 2.7	10.8 ± 3.2	17.6 ± 3.0	***
Theodoxus fluviatilis	65.3 ± 8.2	71.1 ± 8.9	34.1 ± 4.9	42.7 ± 5.6	48.3 ± 7.8	23.8 ± 2.3	22.7 ± 3.4	19.8 ± 2.3	***
Radix peregra	39.5 ± 5.9	40 ± 0.1	14.9 ± 1.4	20.9 ± 3.7	25.6 ± 2.3	12.2 ± 1.6	13.1 ± 1.4	13.3 ± 2.5	***
Crustacea									
Idotea baltica	62.2 ± 14.0	53.3 ± 12.3	10.5 ± 1.9	34.4 ± 5.0	22.6 ± 4.8	9.1 ± 2.0	12.2 ± 2.8	5.5 ± 1.2	***
Gammarus spp.	81.9 ± 9.0	120.9 ± 12.3	102.3 ± 14.2	88.7 ± 14.8	212 ± 22.0	40.8 ± 5.8	45.0 ± 7.9	40.8 ± 9.4	***
Iaera spp.	28.1 ± 3.8	38.7 ± 4.5	35.4 ± 7.9	22.5 ± 3.4	57.1 ± 12.7	25.6 ± 4.5	24.5 ± 4	8.8 ± 1.9	***
Leptocheirus pilosa	2.9 ± 0.8	0.8 ± 0.3	0.2 ± 0.1	1.1 ± 0.3	0.4 ± 0.2	0.6 ± 0.3	0.4 ± 0.2	1.0 ± 0.5	*
Polychaeta									
Hediste diversicolor	0.1 ± 0.1	0.3 ± 0.2	0.8 ± 0.5	0	0.2 ± 0.1	0.5 ± 0.4	1.6 ± 0.9	0	*
Marenzelleria viridis	0	1.0 ± 0.1	0.7 ± 0.4	0.1 ± 0.1	0.3 ± 0.2	0	1.4 ± 0.7	0	***
Turbellaria	0.7 ± 0.3	5.7 ± 1.8	5.8 ± 2.3	1.4 ± 0.6	3.7 ± 1.1	1.0 ± 0.5	4.5 ± 3.2	0.1 ± 0.1	***
Nemertinea									
Prostomatella obscura	0.8 ± 0.4	7.9 ± 2.4	15.6 ± 4	1.3 ± 0.6	14.4 ± 3.5	4.1 ± 1.7	17.6 ± 6.9	1.7 ± 0.8	***
Hirudinea									
Piscicola geometra	4.7 ± 1.0	3.2 ± 0.7	1.8 ± 1.4	2.8 ± 0.6	4.4 ± 0.8	0.8 ± 0.2	1.0 ± 0.4	0.5 ± 0.3	***
Priapulida									
Halicryptus spinulosus	0.3 ± 0.2	0.4 ± 0.2	0.2 ± 0.2	1.7 ± 0.5	0.3 ± 0.2	0.2 ± 0.2	1.0 ± 0.5	0.8 ± 0.7	*
Insecta									
Chironomidae	3.3 ± 1.4	0.8 ± 0.4	0.8 ± 0.3	4.6 ± 1.1	1.7 ± 0.6	2.6 ± 0.9	1.0 ± 0.4	4 ± 1.4	*

Species with non-significant differences between patches are left out. *P*-values indicate differences in the abundance of each taxon between the different treatments. Sample size = 80, sample area 0.04 m^2 *** $P \leq 0.001$, * $P \leq 0.05$ *F*, Fucus; *FM,* Fucus and mussels; *M*, mussels of mixed size; *AA*, artificial algae; *AAM,* artificial algae with mussels; *SP*, small patches; *SM*, mussels of small size; *BR*, bare rock

and the small mussel patches (SP; 10 × 10 cm) contained significantly fewer individuals than any other treatment type. The patches with artificial algae and mussels (AAM) had a higher individual abundance than other treatments except patches with *Fucus* and mussels (FM) and patches with *Fucus* (F). FM differed from all other patches except patches with *Fucus* (F), artificial algae (AA) and artificial algae with mussels (AAM) (Tukey, $P \leq 0.05$). Patches with two engineering species (*Fucus* and mussels, FM, artificial algae and mussels, AAM) contained a higher invertebrate abundance than all patches with solely mussels, but the patches with *Fucus* and mussels (FM) did not significantly differ from patches with single algal structures (AA, F). The maximum number of species (20) was found in the mussel patches (M).

In the naturally occurring patches, dense and intermediately dense mussel patches contained several species that were absent in the *Fucus* patches (*Marenzelleria viridis*, *Mya arenaria*, *Praunus inermis* (Rathke)) or only occurred in very few cases (*Hediste diversicolor*, *Radix peregra* (O.F. Müller), *Prostomatella obscura,* Turbellaria; Table 3). The mussel patches with intermediate density contained the highest species number (Fig. 2a), while the dense mussel patches showed the highest individual abundance excluding blue mussels (Fig. 2b). The intermediately dense mussel patches also contained more individuals than the *Fucus* patches (Fig. 2b). The biomass of mussels (DW soft tissue) in the natural samples differed significantly between categories (ANOVA, $F_{3,\ 36} = 137.6$, $P \leq 0.001$), but no differences could be seen between patches with sparse mussel and patches with *Fucus*.

The assemblages associated with different ecosystem engineers

The global ANOSIM pair-wise comparison between all natural patch types revealed differences between patch type and fauna (Fig. 3a; $P < 0.01$ for all pairs ANOSIM global $R = 0.72$, $P < 0.001$). The largest differences were found between *Fucus* and dense mussel patches ($R = 0.999$, $P < 0.001$) (Fig. 3a). The similarity percentages (SIMPER) of species contributions showed an average species dissimilarity of 45% between dense mussel beds and nearby *Fucus* stands with *Hydrobia* spp., *Gammarus* spp. and

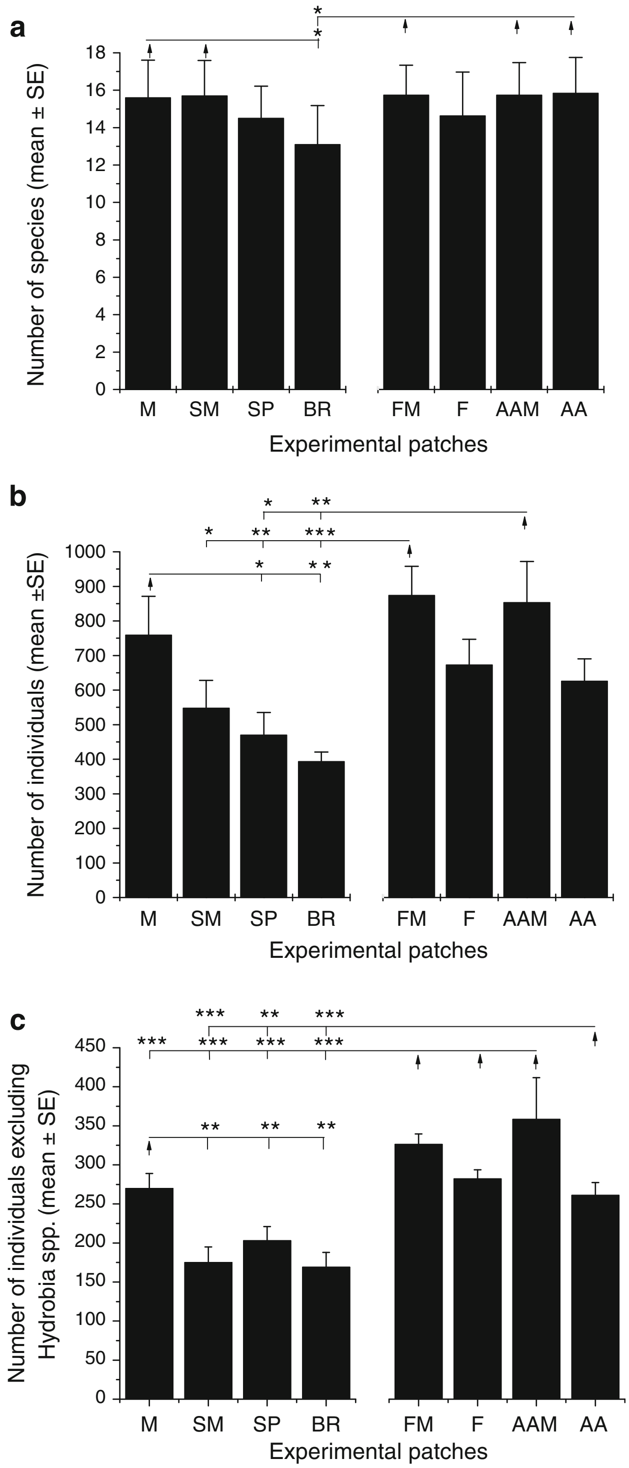

Fig. 1 Number of species (**a**), individuals (**b**) and individuals excluding *Hydrobia* spp. **c** (mean ± SE) in the different treatments (numbers exclude blue mussels). *Lines* above *bars* indicate significant differences between treatments. *Arrows* above *bars* indicate treatments with significantly higher values as shown by the Tukey post hoc test. *Bars* to the *right* include treatments where algal structures were present. $P = * \leq 0.05$, $** \leq 0.01$, $*** \leq 0.001$. *F* Fucus, *FM* Fucus and mussels, *M* mussels of mixed size, *AA* artificial algae, *AAM* artificial algae with mussels, *SP* small patches, *SM* mussels of small size, *BR* bare rock

Macoma balthica (L.) showing largest dissimilarity between the two engineering species with a higher abundance in mussel beds compared to *Fucus*. Also sparse and dense mussel samples displayed a dissimilarity of 42% with the same species being more abundant in dense patches, whereas remaining combinations had an average species dissimilarity of 25–30%.

Likewise, the nMDS plot of the main components in the experimental patches; *Fucus* (F), artificial algae (AA), mussels (M) and bare rock (BR) showed differing assemblages (Fig. 3b; ANOSIM global $R = 0.507$, $P < 0.001$). The mussel patches (M) and bare rock (BR) patches were clearly grouped differently, whereas the patches with *Fucus* (F) and artificial algae (AA) showed a partial overlap (Fig. 3b). In the pair-wise test, the most noticeable dissimilarity was found between mussel patches (M) and *Fucus* patches (F) and between the bare rock patches (BR) and patches with two engineering species (Table 4; $R = 0.759$, $P < 0.001$). Differences between mussel and *Fucus* patches were mainly caused by *Idotea baltica* (Pallas)*, Radix peregra, Theodoxus fluviatilis* (L.)*, Prostomatella obscura* and *Gammarus* spp. as revealed by the SIMPER analysis. *P. obscura* and *Gammarus* spp. were more common in mussel patches, whereas the others occurred more frequently in *Fucus* patches.

Diversity parameters in the experimental and natural mussel patches

When the composition of functional groups in all experimental treatments was compared, the patches were grouped differently depending on the presence/absence of blue mussels (Fig. 4; ANOSIM global $R = 0.625$, $P < 0.001$). The patches with algal structures (AA and F) also grouped closely together, whereas the bare rock treatments (BR) grouped separately from all other treatments. The functional richness in the patches measured as the number of functional groups was significantly lowest in the bare rock (BR) patches compared to all other patches (Fig. 5a; ANOVA, $F_{7,72} = 5.02$, $P < 0.001$) but with no other differences between patches. When diversity was measured as the Shannon heterogeneity index (H′), patches with *Fucus* had the highest diversity index (1.74), whereas it was lowest in the patches with mussels (1.37) (Fig. 5a; ANOVA, $F_{7,72} = 2.54$, $P < 0.05$). Species richness correlated positively with the mussel biomass (Spearman, $r_s = 0.66$, $P < 0.001$) but showed no correlation with the biomass of filamentous algae or fucoids found in the experimental patches (Spearman, $r_s = -0.064$, $P = 0.575$ respectively $r_s = -0.016$, $P = 0.89$).

In the natural blue mussel patches, the patches with dense mussels and intermediately dense mussels had a significantly higher number of functional groups compared

Table 3 Average abundance of macrofauna (ind. 0.04 $m^2 \pm$ SE) in the natural mussel patches and *Fucus* patches

Taxon	Sparse	Int dense	Dense	Fucus	*P* value
Mollusca					
Mytilus edulis	258.5 ± 34.7	898.2 ± 84.9	2373.6 ± 125.5	323.5 ± 67.7	***
Mya arenaria	0.3 ± 0.2	2.5 ± 0.5	10 ± 1.2	0	***
Cerastoderma glaucum	6.6 ± 1.4	3.6 ± 0.8	6.2 ± 1	1.4 ± 0.5	***
Macoma baltica	123.4 ± 29.5	45.9 ± 4.5	218.7 ± 11.4	46.4 ± 4.5	***
Hydrobia spp.	45.8 ± 7.8	160.4 ± 27.6	556.1 ± 102.1	54.1 ± 12.2	***
Potamopyrgus jenkinsi	30.5 ± 5.5	54 ± 12.6	179.5 ± 45	28.9 ± 3.8	***
Theodoxus fluviatilis	9.7 ± 2.2	22 ± 1.5	33.2 ± 2.2	16.4 ± 4.1	***
Radix peregra	2.2 ± 0.8	2.9 ± 0.7	1.3 ± 0.5	0.3 ± 0.2	**
Limapontia capitata	0.4 ± 0.2	1.8 ± 0.5	0.6 ± 0.5	0.2 ± 0.1	**
Crustacea					
Gammarus spp.	138.7 ± 25	164.9 ± 16.5	480.1.2 ± 38.7	108.8 ± 17.8	***
Iaera spp.	25 ± 6.3	90.4 ± 11.5	92.2 ± 13.8	6.3 ± 0.9	***
Idotea baltica	14.7 ± 2.2	13.1 ± 2.6	2.2 ± 0.8	10.4 ± 1.9	***
Balanus improvisus	19.8 ± 4.5	54.3 ± 6.2	80.8 ± 6.6	5.7 ± 1.5	***
Polychaeta					
Fabricia stellaris	19.7 ± 4.6	24.7 ± 3.3	19.2 ± 3.5	5.9 ± 1.5	***
Hediste diversicolor	0.4 ± 0.3	4.6 ± 0.8	12.3 ± 4.1	0.7 ± 0.5	***
Marenzelleria viridis	0	0	0.6 ± 0.3	0	*
Oligochaeta	18.4 ± 4.6	10.5 ± 3.1	24.2 ± 3	2.8 ± 0.8	***
Nemertinea					
Prostomatella obscura	2.4 ± 0.8	10.8 ± 1.8	7.1 ± 0.9	1.5 ± 0.9	***
Nematoda	2.4 ± 1	5 ± 1.1	13.7 ± 3.0	5.4 ± 2.3	***
Ostracoda	2.8 ± 0.5	6.4 ± 1.6	35.6 ± 8.5	2.8 ± 2.8	***
Insecta					
Chironomidae	11.7 ± 2.2	8.8 ± 1.4	5.2 ± 1.4	22.6 ± 4.2	***

Species with non-significant differences between patches are left out. *P*-values indicate differences in the abundance of each taxon between the different patches. Sample size = 40, sample area 0.04 m^2. Int dense = intermediately dense *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$

to the sparse mussel patches and *Fucus* patches (Fig. 5b; ANOVA, $F_{3,\ 36} = 13.87$, $P < 0.001$). The H′ index was highest in the intermediately dense mussel patches (2.13) (Fig. 5b; ANOVA, $F_{3,\ 36} = 10.85$, $P \leq 0.001$). Species number peaked at a mussel biomass of 4 g patch^{-1}, thereafter showing a decline (Fig. 6a), whereas the number of individuals showed a constant increase with mussel biomass (Fig. 6b).

Discussion

This study demonstrates the importance of blue mussel beds to sublittoral hard bottom ecosystems and shows experimentally that rocky shore mussels offer an important habitat for a rich associated fauna. In the northern Baltic, a loss or a large-scale degradation of blue mussel communities (Westerbom et al. 2002) would result in community diversity loss, even collapse, as there are no replacing biological structures with the same function. As shown in this study, the invertebrate communities found on the shores of the northern Baltic Sea are strongly determined by the presence of blue mussels. Results also indicate that fluctuations in blue mussel populations and changes in the demography and size structure of blue mussels, as well as the presence/absence of algal structures, affect invertebrate abundance and species composition on these marginal rocky shores. Our results suggest that also marginal and fluctuating blue mussel beds have an indisputable function, largely determining biodiversity on northern Baltic rocky shores. Our research clearly demonstrates that blue mussels, also at the very edge of their range, form highly important structures and should by all means be included in national underwater monitoring programmes around the Baltic Sea.

Blue mussels and algae as ecosystem engineers

The recolonization of our experimental units was not random since the high-complexity habitats (FM, AAM, M, AA, F) attracted the highest heterogeneity in terms of individual abundance. There were significant differences in the faunal composition between the different mussel patch structures (Fig. 3), indicating that changes in the demography and coverage could affect the faunal composition in the

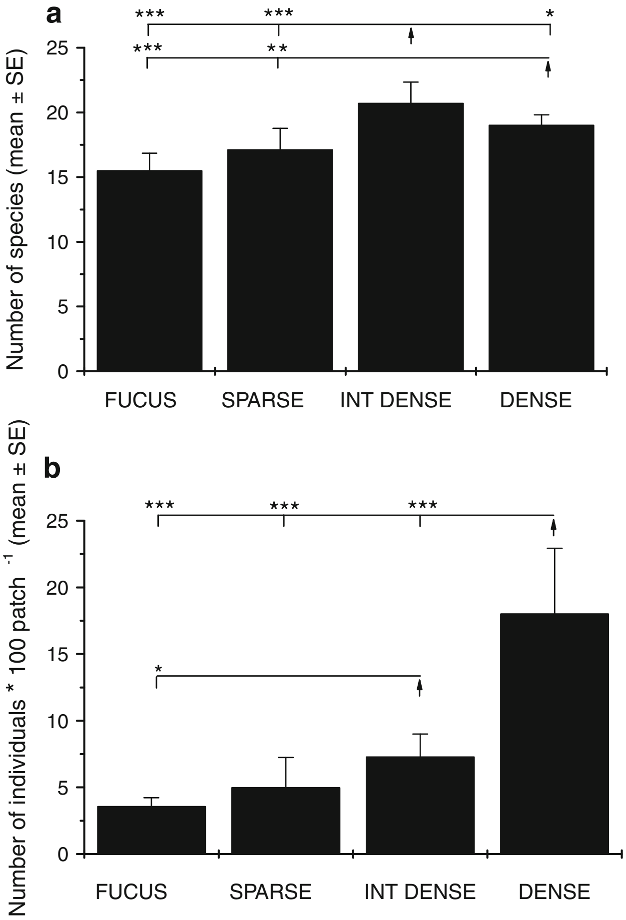

Fig. 2 Number of species (**a**) and individuals × 100 (**b**) (mean ± SE) in the natural patches. *Lines* above *bars* indicate significant differences between treatments. *Arrows* above *bars* indicate treatments with significantly higher values as shown by the Tukey post hoc test. *Int dense* intermediately dense. P = * ≤ 0.05, ** ≤ 0.01, *** ≤ 0.001

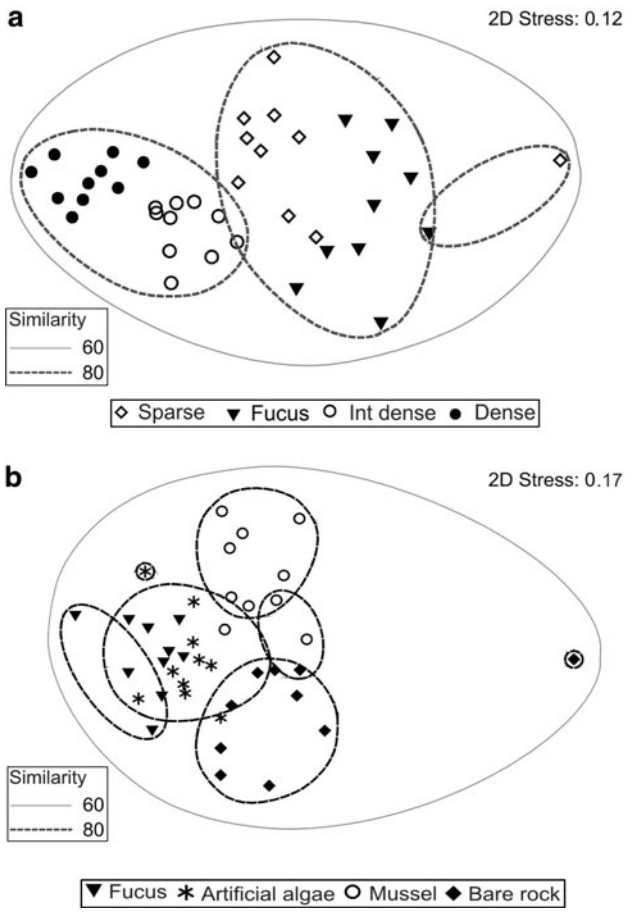

Fig. 3 nMDS ordination of the faunal assemblages in the natural patches (**a**) and experimental patches with the main components (**b**) with superimposed clusters (complete linkage) based on Bray–Curtis similarities at levels of 60% (*continuous line*) and 80% (*dashed line*). *Int dense* intermediately dense

northern Baltic Sea. The presence of blue mussels facilitated the abundance of typical soft-bottom species such as annelids, nemerteans and Turbellaria in the experimental units and reduced the spatial dominance of mobile herbivores and bivalves (excluding *Mytilus*) that were more common in the *Fucus* patches.

The same patterns were found in the natural patches with the exception of a higher abundance of large bivalves (>0.8 cm). In our experiment, bivalves other than blue mussels (especially *Macoma balthica*) were generally more abundant in patches lacking mussels of big size compared to other patch types (Table 2). This suggests negative interactions in the form of inhibition of species with planktonic larvae due to suspension feeding activity by blue mussels (Commito and Boncavage 1989; Thiel and Ullrich 2002). Many mussel species also settle on filamentous structures, which may explain the high juvenile bivalve abundance in the treatments with artificial algae (Littorin and Gilek 1999; Westerbom and Jattu 2006, Westerbom et al. 2008). Mobile adult *M. balthica* individuals were, nonetheless, extremely common in blue mussel patches in both experimental and natural patches showing that mat matrix among blue mussels offers a suitable habitat for *M. balthica* but may inhibit pelagic settlement. Both *M. balthica* and *Cerastoderma glaucum* (Poiret) can potentially switch between suspension and deposit feeding modes in the Baltic Sea (Ólafsson 1986; Hawkins et al. 1990). The modification of post-larval events is an important mechanism by which mussels act as ecosystem engineers due to altered sediment transport (Commito et al. 2005). Differences in the abundance of functional groups in treatments containing mussels vs. treatments without mussels may be explained mainly by a higher number of sessile filtration feeders in the treatments containing mussels as the mussel shells provide a large amount of colonization area (Fig. 4).

In natural samples, the number of species showed an upward trend peaking at the intermediately dense mussel patches and thereafter declining (Fig. 6a). This suggests

Table 4 ANOSIM *R*-values for pair-wise comparisons between experimental treatments

	F	AAM	AA	SM	SP	M	BR
FM	0.29	0.12*	0.42	0.45	0.54	0.33	0.76
F		0.52	0.15*	0.52	0.45	0.64	0.52
AAM			0.53	0.38	0.53	0.23	0.74
AA				0.43	0.28	0.55	0.42
SM					0.12$^{\text{ns}}$	0.14*	0.24
SP						0.28	0.10$^{\text{ns}}$
M							0.59

F Fucus, *FM* Fucus and mussels, *M* mussels of mixed size, *AA* artificial algae, *AAM* artificial algae with mussels, *SP* small patches, *SM* mussels of small size, *BR* bare rock

$N = 80$, Global r 0.39, $P < 0.001$

* $P < 0.05$, otherwise $P < 0.01$ or when indicated ns

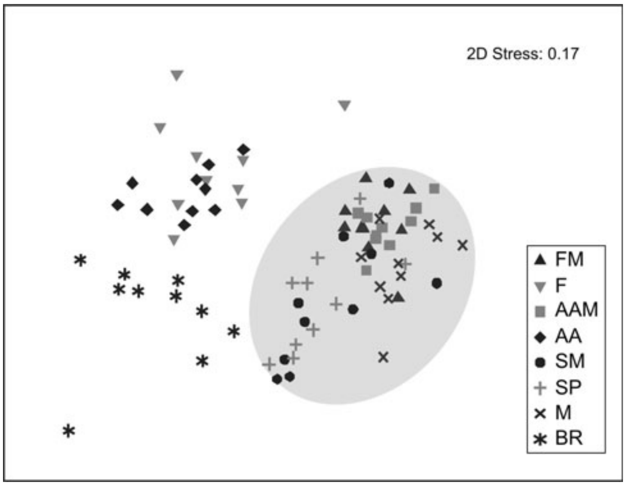

Fig. 4 nMDS ordination of the functional groups in the experimental treatments. *Symbols* in *gray* area mark treatments containing mussels. *F* Fucus, *FM* Fucus and mussels, *M* mussels of mixed size, *AA* artificial algae, *AAM* artificial algae with mussels, *SP* small patches, *SM* mussels of small size, *BR* bare rock

that the structure of blue mussels is an important determinant for diversity. The intermediately dense mussel patches probably offer the highest spatial complexity with both a large surface area for attachment of algae and associated species as well as interstices between shells functioning as hideouts for mobile fauna and collectors of organic sediment. This is supported by other studies that have shown that fractal dimension values in mussel beds are highest at intermediate values of mussel cover and density (Snover and Commito 1998). The sediment in the mussel matrix functions as an important habitat for bottom dwelling worms and constitutes a source of nutrition for mobile detrivores (Bick and Zettler 1994). This was clearly seen in this study where infauna (polychaetes, nemerteans, Turbellaria) was significantly associated to patches with mussels

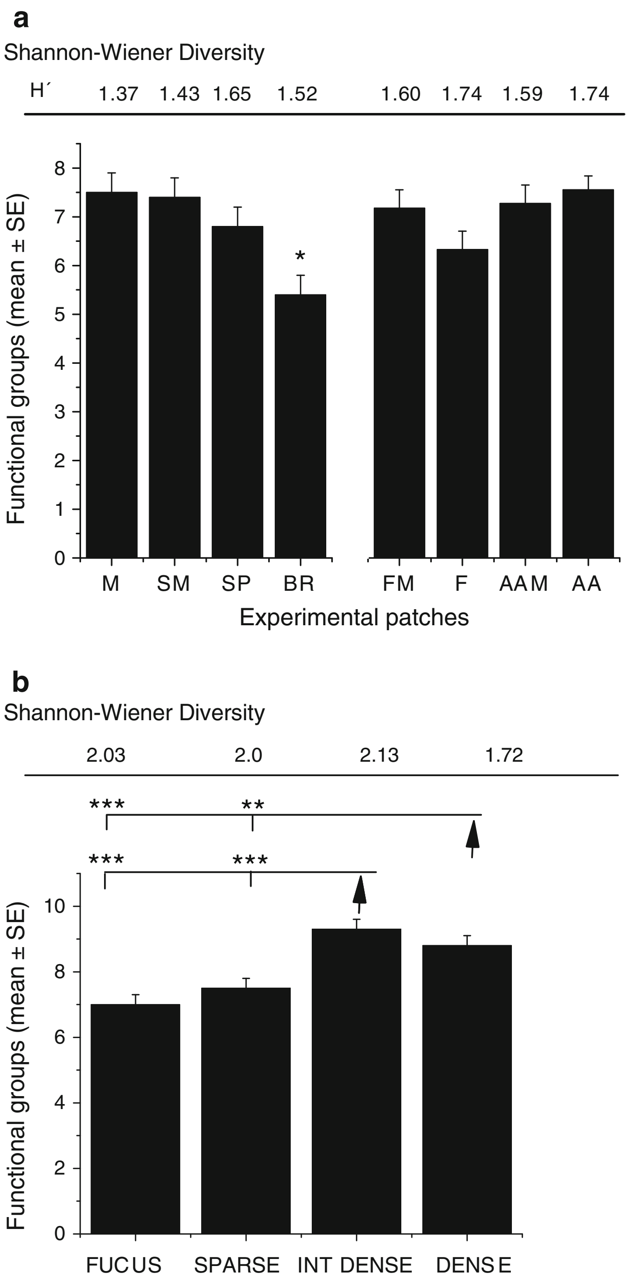

Fig. 5 Number of functional groups and Shannon Wiener diversity (H′) in the experimental patches (**a**) and the natural patches (**b**). *Lines* above *bars* indicate significant differences between treatments. *Arrows* above *bars* indicate treatments with significantly higher values as shown by the Tukey post hoc test. *Bars* to the *right* (**a**) include treatments where algal structures were present. $P = * \leq 0.05$, $** \leq 0.01$, $*** \leq 0.001$. See text for details. *F* Fucus, *FM* Fucus and mussels, *M* mussels of mixed size, *AA* artificial algae, *AAM* artificial algae with mussels, *SP* small patches, *SM* mussels of small size, *BR* bare rock, *Int dense* intermediately dense

(Tables 2, 3). The higher abundance of associated fauna in mussel beds with a high mussel density (Fig. 6b) may be explained by functional attributes of the mussels such as filtration, nutrient excretion and biodeposition offering

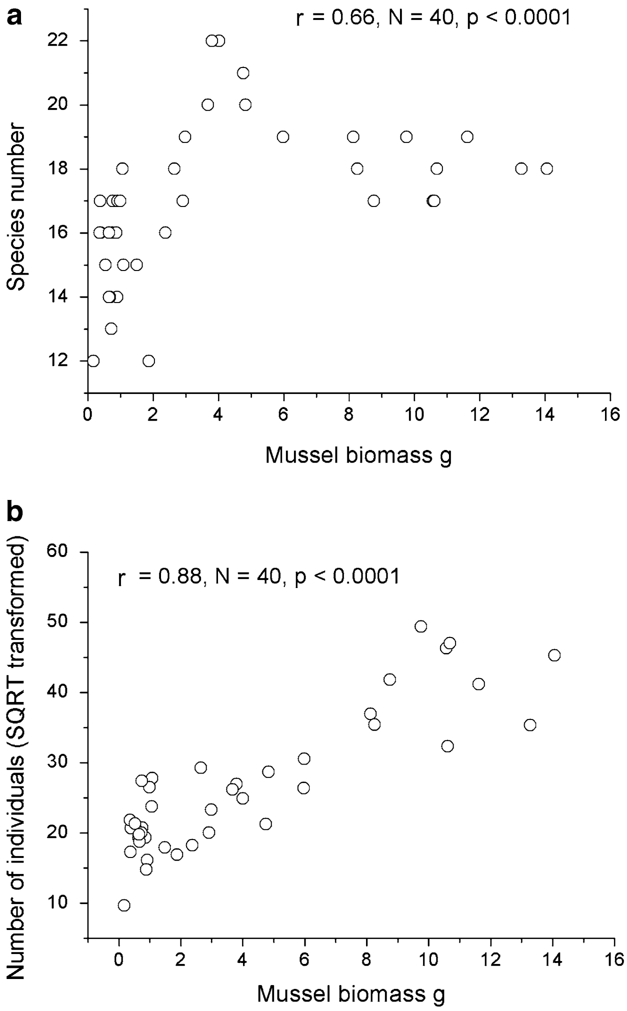

Fig. 6 Relationship between mussel biomass and number of species (**a**) and biomass and number of individuals (**b**) (mean ± SE) in the natural patches

important resources to other species (Norling and Kautsky 2007). However, a very dense mussel bed lowers the amount of free space, outcompeting algae and other important structures that contribute to increased species diversity. Our results are supported by earlier studies where species diversity in blue mussel communities has been related to the structure of the mussel bed in terms of age of mussels and structure of space among shells as explained by the trapping of sediments in the interstitial spaces between mussels in older patches (Suchanek 1980; Tsuchiya and Nishihira 1986; Norling and Kautsky 2007).

In the natural mussel beds, the dense mussel patches showed a fivefold number of individuals compared to the *Fucus* patches and the sparse mussel beds (Fig. 2b). In the experimental patches, the patches containing mussels (M) also outnumbered the *Fucus* patches in terms of individual density although the results were not as clear-cut as in the natural samples, possibly due to the short duration of the experiment. Our results therefore imply that the faunal diversity found within dense mussel patches in the northern Baltic is well comparable to that found within *Fucus* habitats that have received considerably more attention from Baltic scientists (see also Norling and Kautsky 2008). However, the lower species and individual number in the *Fucus* patches compared with mussels may have been due to the small-scale approach in this experiment since *Fucus* usually forms belts much larger than the sampled isolated habitat patches. Also, the whiplash effect of *Fucus* (Kiirikki 1996b) may have lowered the species diversity and individual abundance in the immediate surroundings of the *Fucus* patch.

The additive effects of multiple engineer species and the role of bioengineers

Although most studies find positive associations between habitat structure and faunal diversity, these relationships are not always clear. Nevertheless, the results of our study showed a positive relationship between habitat complexity and diversity in blue mussel patches on a small within-shore scale. Our results suggest that the increased physical complexity, as a result of algal presence in mussel beds, affects species composition and increases individual abundance of associated fauna in mussel beds (Figs. 3a–b, 1c). Our results also indicate that the structural functions (physical complexity, epiphytes and microflora) are highly important since diversity did not differ between the *Fucus* and artificial algal treatments (Fig. 1a). The biological effects of *Fucus* may even have negative effects on the associated fauna since *Fucus* produces several chemical substances as a defense to grazing herbivores and epiphytes (Jormalainen and Ramsay 2009). Within the blue mussel communities, *Fucus* seems to enhance physical conditions by providing surface and stable substrate and thereby has a positive effect on the abundance of bed inhabitants. In the experimental patches with both engineering species, especially mobile algal herbivores were abundant showing that mixed patches of mussels and algae embody a high qualitative complexity in terms of biological and physical resources. Pair-wise differences between structurally similar patches (BR vs. SP, SM vs. M and AAM vs. FM) were small (Fig. 4; Table 4), and the highest dissimilarity was found between patches with highest (FM, AAM) and lowest heterogeneity (BR) (Fig. 4). All species that were present in either *Fucus* or mussel patches were also found in the joint presence of both engineering species.

The division of species into functional groups revealed the high functional value of the bioengineered patches. In this study, the number of functional groups varied between 7 and 9 in all the habitats containing *Fucus* or mussels in comparison with the bare rock habitats that contained less than 6 functional groups on average, confirming the roles of mussels and *Fucus* as biodiversity hot spots in the northern Baltic Sea. Some of the functional groups, such as mobile carnivores, were completely absent in bare rock patches.

In conclusion, the blue mussel is an example of a species that facilitates the establishment and maintenance of unique invertebrate communities by reducing physical disturbance to tolerable levels, by altering water flow and sedimentation processes, by providing nutrients (feces and pseudofeces) and hideouts to mobile fauna and by affecting post-larval events. Therefore, a lowered salinity in the Baltic Sea that affects the demography and coverage of blue mussels in the northern Baltic Sea will have profound effects on these ecosystems since a replacement by a functionally similar indigenous species is very unlikely. Identifying important facilitators as well as the mechanisms through which they may benefit their neighbors enables these species to be taken into consideration when making conservational efforts and increase our understanding of the dynamics and organization of rocky sublittoral communities. Our study shows that blue mussel beds at the edge of their distributional range, despite their temporally low biomass, fluctuating coverage and small individual size, promote and maintain a species-rich community and alone uphold a rich faunal community.

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