



Structural and functional effects of *Mytilus edulis* on diversity of associated species and ecosystem functioning

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ABSTRACT: Habitat-modifying species such as *Mytilus edulis* strongly impact both community structure and ecosystem functioning through positive or negative interactions with other species and by changing physical and biological conditions. A study of natural patches of mussels showed that C and N content of sediment was higher in mussel patches compared to the surrounding sand community. Species richness and biomass of associated macrofauna and -flora was enhanced even by the presence of single mussels and increased rapidly with patch size up to about 150 cm², while no change in sediment meiofauna was found. In order to separate the effects of structure and function of *M. edulis*, a manipulative field experiment was performed with constructed patches of cleaned live mussels or intact empty shells. After 3 mo colonisation, the number of associated species in both treatments approached those in natural mussel patches, indicating that species richness was mainly due to physical structure. Abundance and biomass of associated flora and fauna were higher if live mussels were present because mussel biodeposition and nutrient regeneration supplied limiting resources and increased carrying capacity. Species composition was also affected. Complexity and biodiversity increased with time, especially if *Fucus vesiculosus* plants established themselves. Measurements of community metabolism showed that the associated community found in mussel patches depends on mussel biodeposition for 24 to 31 % of its energy demand. Thus, the energy balance of the community is dependent on the function of live mussels.

KEY WORDS: Biodiversity · Ecosystem functioning · Facilitation · Species interactions · Habitat modification · *Mytilus edulis* · Community metabolism

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INTRODUCTION

Dominant habitat-forming and -modifying species are common in both terrestrial and aquatic systems (Hooper & Vitousek 1997, Tilman et al. 1997). These habitat-modifying species can have positive or negative effects on other species by changing physical and biological conditions in the local environment, thereby creating habitats that sometimes can characterize entire ecosystems. Often they provide living space and favourable conditions for other species, causing net facilitation of biodiversity of associated species. The facilitation effects are likely to vary across environmental gradients, becoming more important in harsher

environments as habitat-modifying species facilitate conditions for other species by reducing stress or providing resources (Rhoads & Young 1971, Bruno et al. 2003, Crain & Bertness 2006). Frequently, these effects are a precondition for the existence of other species in a specific environment.

It has long been recognized that physical habitat structure directly controls the distribution and abundance of species by providing substrate for colonisation as well as refuges from competition, predation and disturbance. Not until recently has the biological generation of habitats and the positive interactions that occur within habitats been incorporated in ecological theory (see review Bruno & Bertness 2001, Bruno et al.

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2003). Direct positive interactions have been shown to have a large potential for controlling species diversity (Hacker & Gaines 1997), but the relative importance of positive interactions compared with other interactions and processes in determining community patterns remains unclear (Menge 2000).

In the marine environment, there are several examples of individual dominant species that modify the habitat and thereby have strong effects on biodiversity, e.g. sea grasses, kelps, coral reefs and bivalve beds. Mechanisms whereby these habitat-modifying and forming species influence the marine communities can be divided into 2 groups based on physical structure or biological activity. The common blue mussel *Mytilus edulis*, a reef-forming suspension feeding bivalve, can modify the environment in many different ways and thereby influence the structure and abundance of its associated community (Table 1).

Habitat modification by *Mytilus edulis* has in most cases been reported to result in highly diverse assemblages on hard substratum (Suchanek 1985, Tsuchiya & Nishihira 1986, Lintas & Seed 1994) and in sandy sediment habitats (Dittmann 1990, Albrecht & Reise 1994, Svane & Setyobudiandi 1996, Ragnarsson & Raffaelli 1999), although in some cases *M. edulis* may monopolise available substrate and inhibit the presence of other species or displace other benthic fauna (Suchanek 1985). Most previous studies have investigated the effects of mussels on macrofauna, while few studies have dealt with associated meiofauna (Radziejewska 1986, Dittmann 1990) and macroalgae (Albrecht & Reise 1994).

Mytilid mussels are a conspicuous component in many coastal areas and estuaries, often forming exten-

sive beds comprising both live mussels and dead shells, which exert significant effects on benthic-pelagic coupling and energy flow through their filtration activities (Kautsky & Evans 1987, Newell 2004). These beds have a characteristic appearance and species composition of fauna and flora, but relatively little is known regarding the relative importance of the structural properties or biological activity of the mussels in determining the biodiversity and ecological functioning of the community of associated species (Ragnarsson & Raffaelli 1999, Chintiroglou et al. 2004). Several underlying mechanisms have been proposed which could apply to both hard and soft sediment mussel beds. Tsuchiya & Nishihira (1986) emphasize structural complexity, while Lintas & Seed (1994) emphasize mussel density as having direct effects on diversity of mussel (*Mytilus edulis*) bed assemblages. Like most other studies, these involve general facilitation processes focusing primarily on the physical structural aspects of habitat modification. Few studies have tried to separate the structural and functional effects in habitat modification and even fewer have studied the effects on ecosystem functioning.

The aim of the present study was to separate physical structural effects from biological functional effects and quantify their respective effects on patterns of associated macrofauna and -flora in *Mytilus edulis* patches in order to understand the underlying mechanisms for the formation of the associated community. This was accomplished using a whole system approach by constructing patches of cleaned living mussels and intact empty mussel shells in the field. The development of communities of associated species and accumulation of organic matter under these experimental conditions was compared with that in the communities found in naturally occurring mussel patches and in a control area without mussels. Unlike previous studies, the community metabolism (Odum 1969) of the developed communities was studied in order to quantify ecosystem functioning. To understand the spatial scales on which mussels may affect biodiversity, we also compared the composition of associated species in naturally occurring mussel patches of different sizes.

Our main hypothesis was that empty mussel shells and live mussels have different effects on biodiversity of associated species, and hence that: (1) species richness, abundance and composition differ between patches of empty shells and live mussels; (2) the accumulation of organic matter in the sediment is higher in live mussel patches compared to that in empty shells; (3) live mussel patches support higher abundances of deposit feeding fauna such as Oligochaeta and Polychaeta; and (4) the functioning of the system in terms of community metabolism differs between the empty shell and live mussel patches.

Table 1. Structural and functional characteristics of *Mytilus edulis* beds that may influence patterns of biodiversity

Characteristics	Source
Structure (physical traits)	
Secondary substrata	Tsuchiya & Nishihira (1986), Albrecht & Reise (1994)
Interstitial cavities	Yager et al. (1993)
Sediment trap	Yager et al. (1993)
Sediment stabilization	Young (1983)
Boundary layer	Frechette et al. (1989)
Function (biological traits)	
Filtration currents	Laihonen & Furman (1986)
Physical activity	Laihonen & Furman (1986)
Biodeposition	Kautsky & Evans (1987)
Nutrient regeneration	Kautsky & Wallentinus (1980), Prins et al. (1998)
Water clearance	Newell (2004)
Predation/grazing	Newell (2004)
Direct food source	Kautsky (1981)

MATERIALS AND METHODS

Site description. The study was conducted at Vanarna, south of Tjärnö on the west coast of Sweden, during July 2003 and May and August 2004. Here, mussel beds are restricted largely to intermediately wave-exposed hard bottoms and intertidal sediments. The distribution of *Mytilus edulis* is restricted to shallow water by intense predation from starfish *Asterias rubens* and shore crab *Carcinus maenas*. On shallow sediments, *M. edulis* are found in mussel beds and in more fragmented forms of patchy 'islands', which are often substrata for macroalgae, e.g. *Fucus* spp. This study was performed in a shallow sound, protected from large waves, but with a tidally generated water flow that swept the area where natural mussel patches occurred between 0.5 and 1 m mean low water (MLW) depth on sandy sediment. The normal tidal range in this area is approximately 25 cm and salinity varies between approximately 20 and 30 psu.

Biodiversity in natural *Mytilus edulis* patches. The first study in July 2003 established the relationship between biodiversity of associated species, accumulation of organic matter by *Mytilus edulis* and patch size in naturally occurring patches. Patches ranging from 16 to 245 cm² were sampled on sandy sediment at a depth of 54 to 70 cm below MLW. Duplicate sediment samples for meiofauna and sediment characteristics were collected inside, and 30 cm outside (in the water swept area without traces of mussel biodeposits), each mussel patch, using sediment cores of surface area 5.3 cm². From half of the sediment samples, the top 2 cm was collected for sediment characterization and chemical analysis. The other half was preserved in 4% buffered formalin for meiofauna studies. In addition, 5 sediment samples were collected for sediment characterization from a nearby (~10 m) control area without mussel patches. Whole mussel patches, including associated fauna and flora, were collected by scraping off the mussel patch, including 1 cm surface sediment, within a sample frame of 20 × 20 cm into a net bag. These were frozen. After thawing and sieving through a 0.5 mm sieve, the macrofauna samples were sorted for biodiversity determination. With a dissecting microscope, all macrofauna >0.5 mm was identified to family level and, for dominant taxonomic groups, also to species level. Macroalgae were identified to species level, except for *Ulva* sp. and the encrusting algae *Ralfsia verrucosa* and *Hildenbrandia* sp. Meiofauna were extracted by diluting the sediment with water and repeatedly stirring and decanting the supernatant through a set of sieves with 0.040, 0.100 and 1 mm mesh size. The samples were stained with rose bengal before being counted under a dissecting microscope. The 100 µm fractions were used in the meiofauna

diversity studies where the fauna was identified primarily to family level. The sediment was dried to constant weight at 60°C before total carbon and nitrogen were analysed with a LECO Elemental Analyser, model CHNS-932, and were run in duplicate.

Colonisation of constructed shell and mussel patches. In early May 2004, empty mussel shells and live mussels ranging between 6.0 and 7.1 cm in length were collected and cleaned from epibionts. Either 8 live mussels or 8 empty shells were tied together with a piece of string and reassembled into a total of 14 patches (each 15 × 15 cm) that were then anchored with iron rods to a sand bottom at approx. 0.6 m below MLW in an area at the Vanarna site (see above) with natural mussel patches with an average density of approx. 2 m. Three months were allowed for the establishment of associated fauna before the patches were used in the metabolism studies and analysed as described above for macrofauna and flora as well as sediment characteristics (samples were collected inside each patch and at a control area).

Community metabolism. By analysing the magnitude and gross production/ respiration (GP/R) ratios of benthic oxygen fluxes, it is possible to gain insight into factors controlling pathways of carbon at a given location (Giblin et al. 1997). In August 2004, measurements of oxygen flux were conducted *in situ* on the patches of empty shells ('Shells') and cleaned live mussels ('Cleaned') (after 3 mo recolonisation), as well as on the nearby bare sand flat ('Sand') and natural mussel patches ('Natural'). In addition, in order to calculate the weight specific respiration rate of mussels, the measurements included patches of 8 mussels that had been cleaned from attached flora and fauna on the day before. Oxygen measurements were carried out with a polarographic oxygen electrode (WTW 196 Oximeter) equipped with stirrer, after the above patches were enclosed in chambers (Ø = 20 cm, h = 30 cm) made of plexiglass that were pressed 5 cm into the sediment. Measurements were done around noon on a clear day. Water temperature was approximately 20°C. Measurements were taken for approximately 90 min in light followed by 90 min in dark conditions with the chambers covered by black plastic. Maximum variation in O₂ saturation in the enclosures ranged between 80 and 120%, indicating only minor effects of saturation on metabolism. Community metabolism was estimated from the changes in the concentrations of dissolved oxygen in the incubated chambers calculated per hour. The light period was used to calculate the net community production (NP). Community respiration (R) was estimated from changes in oxygen concentration in dark conditions. The sum of R and NP provided estimates of gross production (GP), and the degree of self-maintenance was expressed as the GP/R ratio over 3 h

at midday as well as over 24 h. The GP/R ratio is a dimensionless estimate of the autotrophic capability of a community and a ratio equal to or above 1 on a 24 h basis indicates self-maintenance, while a ratio below 1 indicates a dependence on imports of organic matter (e.g. Odum 1969, Hopkinson & Smith 2004).

Larger mobile fauna (*Carcinus maenas*, *Palaemon elegans*) were enumerated before the chambers were removed, after which samples for sediment organic content were taken and the patches were collected for quantification of fauna and flora as outlined above. In the final calculations, the community metabolism parameters for the associated fauna and flora, and the underlying sediment flora, fauna and microbes were estimated by subtracting the respiration of the mussels and the metabolism of the bare sand surrounding the patches in the enclosures. The resulting values for empty 'Shells', from which values for 'Sand' were subtracted, are a measure of the activity of associated fauna and flora due to mussel shell structure providing attachment surfaces and crevices that trap detritus and are used as refuges. The difference with respect to 'Cleaned' mussels should be due to the biological function of living mussels (i.e. filter feeding, biodeposition, nutrient regeneration, or other species interactions).

Statistical methods. Linear regression (LR) was used to relate organic content (carbon and nitrogen) in sediment and patch size. The relationships between patch size and the abundance of macrofauna and meiofauna as well as the biomass of macrofauna and macroalgae were all tested with LR. In addition, the relationship between macrofauna and macroalgae was analysed using LR. Since curved asymptotic relationships were expected, the species richness of macrofauna, macroalgae and meiofauna in the mussel patch study were related to patch size using nonlinear regression (NR) according to Peak & Quinn (1993).

Comparisons of organic content, meiofauna species richness and abundance between inside and outside patches were tested at the 0.05 significance level by a paired *t*-test (dependent samples) after Cochran's *C*-test of homogeneity was conducted. Organic content data was log-transformed to meet the homogeneity requirement. Differences between the 'Sand' control and mussel patch treatments ('Shell', 'Cleaned' and 'Natural') in terms of macroalgae biomass, macrofauna biomass and abundance, as well as species richness of macroalgae and macrofauna, were tested at the 0.05 significance level by one-way ANOVA after a Cochran's *C*-test of homogeneity was conducted. The differences were then tested with the Student Newman-Keuls (SNK) test. To meet the homogeneity requirement, the biomass data were log-transformed and abundance and species richness data were square root transformed. The significance of the organic con-

tent in response to sampling position in the colonisation study was also tested with ANOVA as above, using log-transformed data. All statistical analyses were performed using Statistica 6.0™ (StatSoft).

RESULTS

Patch study

Sediment

Total organic carbon and nitrogen contents in the sediment significantly increased with increasing patch size, carbon (LR, $p < 0.001$, $r^2 = 0.81$) and nitrogen (LR, $p = 0.001$, $r^2 = 0.77$) respectively (Fig. 1). Significantly higher carbon content (*t*-test, $n = 10$, $t = 2.70$, $p < 0.02$) and nitrogen content (*t*-test, $n = 10$, $t = 2.76$, $p < 0.02$) were found in sediment outside patches compared to

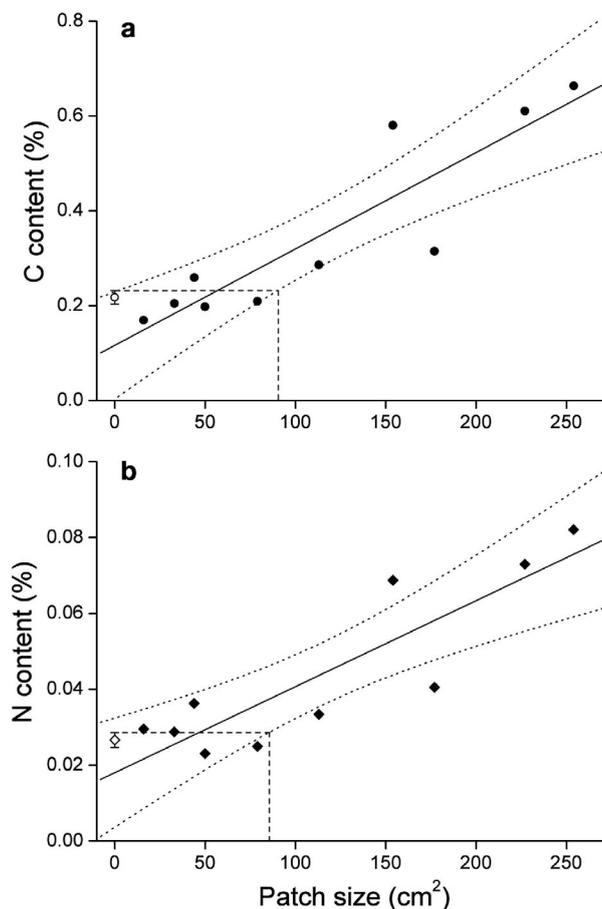


Fig. 1. (a) Carbon (●) and (b) nitrogen (◆) content (%) in sediment of *Mytilus edulis* patches of different sizes, and average carbon (○) and nitrogen (◇) contents in sediment (% ± SE) from the control area without mussels ($n = 5$). Dotted lines: 95% confidence interval. Dashed lines: patch size where content is greater than in the control area

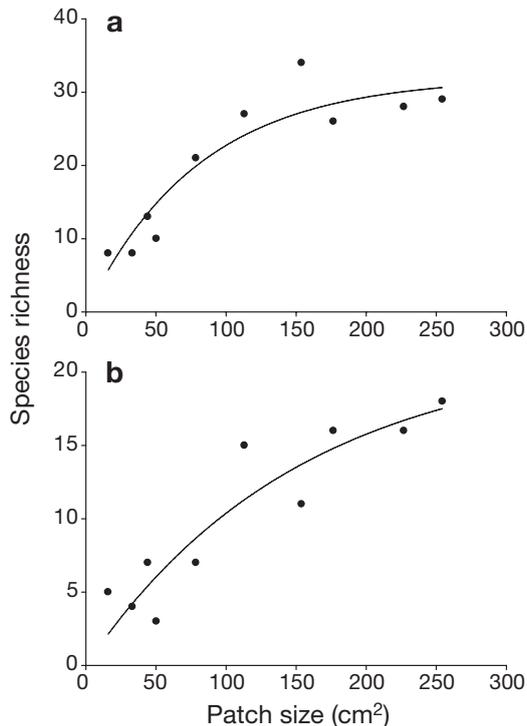


Fig. 2. (a) Macrofauna and (b) macroalgae species richness in *Mytilus edulis* patches of different sizes (i.e. per 400 cm²)

inside patches. In comparison to the sediment control samples, the 95 % confidence interval around the regression line (Fig. 1) showed that mussel patches have higher organic content when patches were larger than 90 cm² (for carbon) and 85 cm² (for nitrogen).

Although carbon content increased faster in relation to patch size than nitrogen content (Fig. 1), the change in C/N ratio was not significant. Within patches, the C/N ratio ranged from 5.7 to 8.6 (average 7.8 ± 0.9 SE), while in the control the average C/N ratio was 7.7 ± 0.9.

Macrofauna and macroalgae

Species richness of macrofauna increased with increasing patch area (NR, $p < 0.001$, $r^2 = 0.88$) (Fig. 2a). The number increased up to a patch size of approximately 150 cm², after which it stabilized at about 30 species. The patch size of 225 cm² used in the metabolism study is thus well over this asymptotic level.

A total of 45 macrofauna species occurred in the *Mytilus edulis* patches, of which a maximum number of 34 species occurred at a patch size of 154 cm². Crustacea (13 species, e.g. *Balanus improvisus*, *Microdeutopus gryllotalpa* and *Corophium volutator*), Gastropoda (8 species, e.g. *Rissoa* sp. and *Littorina littorea*) and Polychaeta (7 species, e.g. *Spirorbis spirorbis* and

Harmothoe imbricata) were the dominant taxonomic groups in all patches. Crustacea also dominated in terms of abundance, due to the high abundance of *Balanus improvisus*.

A total of 23 macroalgae species occurred in the mussel patches. As with the macrofauna, the species richness of macroalgae increased with patch size up to an asymptotic level about 250 cm² (NR, $p < 0.001$, $r^2 = 0.84$) (Fig. 2b). The maximum number of species (18) occurred at a patch size of 254 cm². The dominant species in patches larger than 100 cm² were *Fucus vesiculosus* and *Dictyosiphon foeniculaceus* (43 ± 13% and 38 ± 3% respectively of total biomass) as well as the filamentous algae *Sphacelaria cirrosa*. With increasing biomass of *Fucus vesiculosus*, there was also an increase in attached fauna and flora living on the thallus of this species, e.g. *Elachista fucicola*, *Spermatochnus paradoxus*, *Dynamena pumila*, *Electra pilosa* and *Membranipora membranacea*.

The biomass of macrofauna increased with increasing patch size (LR, $p = 0.02$, $r^2 = 0.50$), and the same pattern was found for the biomass of macroalgae (LR, $p = 0.01$, $r^2 = 0.61$). A relationship between macrofauna density and area was found, although it was not significant (LR, $p = 0.05$, $r^2 = 0.39$). There was also a weak relationship between macroalgae and macrofauna biomass (LR, $p = 0.04$, $r^2 = 0.46$), indicating that these 2 factors may be interdependent.

Meiofauna

A total of 33 meiofauna taxa were found (Table 2). Outside of the patches, 16.6 ± 0.5 (SE) taxa occurred. In the patches, the number of taxa was on average 16.1 ± 1.3, and did not change with patch size. There was no relation between abundance and patch size. In addition, there was no significant difference in number of taxa inside and outside the patches.

Colonisation of constructed shell and mussel patches

Macroalgae

A total of 16 macroalgae species occurred in the 3 mussel patch treatments ('Shell', 'Cleaned' and 'Natural') compared to no algae in the 'Sand' control (Table 3). In the constructed patches 'Shell' and 'Cleaned' live mussels, there were on average 5.7 and 5.4 species, respectively, and in older 'Natural' patches there were 7.0 species. The slowly growing *Cladophora rupestris* and *Chondrus crispus* occurred only in 'Natural', probably because these patches were older. *Polysiphonia fucoides* and *Corallina officinalis* found

Table 2. Average abundance of meiofauna ($10^3 \text{ m}^{-2} \pm \text{SE}$) and average number of taxa in sediment outside and inside *Mytilus edulis* patches of different sizes (n = 10). -: taxon not present

Taxon	Outside		Inside	
	Mean	SE	Mean	SE
Ciliata	0.8	0.5	0.9	0.5
Foraminifera	7	1.6	5	2.6
Porifera	–		0.2	0.2
Protohydridae	14	2.1	13	5.3
Platyhelminthes (total)	12	2.0	8	1.9
Proseriatida	2	0.8	2	0.8
Polycystidae	2	0.7	2	0.8
Other	9	1.6	6	1.2
Rotifera	0.8	0.4	0.8	0.8
Nematoda	548	85	465	100
Nemertinea	0.6	0.4	0.2	0.2
Polychaeta (total)	13	2.6	26	13
Polychaeta sp.	1.1	0.6	1.1	0.6
Protodrilidae	0.6	0.3	0.6	0.3
Capitellidae	8.3	2.1	22	12
Nereidae	0.9	0.6	0.8	0.6
Other (juv.)	1.7	1.1	1.3	0.6
Oligochaeta	–		0.6	0.4
Copepoda (total)	332	41	156	38
Harpacticoida	328	130	3.0	1.0
Tanaida	0.2	0.2	0.2	0.2
Ostracoda (total)	30	8.6	28	10
Pontocyprididae	0.9	0.5	1.7	0.8
Other	29	8.3	27	9.7
Cirripedia: Balanoida	–		1.9	0.8
Amphipoda	–		1.3	0.5
Halacaridae	0.2	0.2	0.9	0.6
Chironomidae	0.4	0.4	1.9	0.9
Gastropoda (total)	129	20	56	27
Hydrobidae	128	21	56	27
Littorina sp.	0.2	0.2	–	
Other	0.8	0.6	0.6	0.4
Bivalvia (total)	138	17	74	21
Cardidae	16	2.2	6	2.7
sp. 1 ^a	49	18	20	60
Other	74	21	48	17
Polyplocophora	–		0.2	0.2
Echinodermata	–		0.4	0.3
Echinoidea	0.4	0.3	1.3	0.9
Mean total abundance	1226	98	842	142
Mean number of taxa	16.6	0.5	16.1	1.3

^aSpecies distinguished but not identified

in 'Shell' and 'Cleaned', respectively, were probably drifting specimens that had become entangled in the patches.

The macroalgae biomass (excluding biomass of the crust-forming species *Hildenbrandia* sp., *Phymatolithon lenormandii* and *Ralfsia verrucosa*) differed significantly among the mussel treatments 'Shell', 'Cleaned' and 'Natural' (ANOVA, $F_{2,18} = 12.39$, $p = 0.001$), with higher biomass in 'Natural' as compared to 'Cleaned' (SNK, $n = 7$, $p < 0.001$) and 'Shell' (SNK, $n = 7$, $p = 0.024$). This was due to the significantly higher bio-

masses of filamentous Phaeophyta (ANOVA, $F_{2,18} = 13.42$, $p = 0.0003$) as compared to 'Shell' (SNK, $n = 7$, $p = 0.004$) and 'Cleaned' (SNK, $n = 7$, $p = 0.0003$), and of *Fucus vesiculosus* in 'Natural' (Fig. 3). In addition, the total biomass in 'Shell' was significantly higher than in 'Cleaned' (SNK, $n = 7$, $p = 0.02$). The biomass of *Dictyosiphon foeniculaceus* (ANOVA, $F_{2,18} = 6.51$, $p = 0.007$) and *Fucus* germlings (ANOVA, 4th-root-transformed, $F_{2,18} = 41.64$, $p < 0.001$) also differed among the treatments, with significantly higher biomasses in 'Shell' as compared to 'Cleaned' (SNK, $n = 7$, $p = 0.01$ and $p < 0.001$ respectively) and 'Natural' (SNK, $n = 7$, $p = 0.01$ and $p < 0.001$ respectively).

The macroalgae biomass in 'Cleaned' live mussels was on average one third of that in empty 'Shell', indicating that mussels have the ability to affect the recruitment and growth of *Fucus vesiculosus* and *Dictyosiphon foeniculaceus* germlings (Fig. 3). The opposite pattern was found for fast-growing Chlorophyta (*Ulva* sp.), which seemed to have been facilitated by *Mytilus edulis* nutrient regeneration. The largest algal biomass with the most diverse macroalgae assemblage

Table 3. Average biomass (g DW m^{-2}) (\pm SE) of macroalgae species in patches of different mussel treatments: 'Shell', 'Cleaned' and 'Natural' (n = 7). +: taxon present but not quantified, -: taxon not present

Taxon	Shell	Cleaned	Natural
Chlorophyta^a	1.7 (0.3)	3.5 (1.0)	5.5 (2.0)
<i>Cladophora rupestris</i>	–	–	+
<i>Ulva intestinalis</i>	+	+	+
<i>Ulva</i> sp.	+	+	+
Phaeophyta^b	28 (7.5)	6.6 (1.0)	76 (27)
<i>Dictyosiphon foeniculaceus</i>	7.2 (3.0)	0.6 (0.2)	1.0 (0.6)
<i>Ectocarpus siliculosus</i>	+	+	+
<i>Fucus vesiculosus</i>	0.4 (0.4)	0.5 (0.2)	34 (16)
<i>Fucus</i> juv.	8.4 (2.2)	0.02 (0.02)	0.9 (0.3)
<i>Sphacelaria cirrosa</i>	+	+	+
<i>Ralfsia verrucosa</i>	+	+	+
Rhodophyta^c	1.5 (0.4)	0.7 (0.2)	3.5 (2.8)
<i>Osmundea truncata</i>	0.5 (0.2)	0.1 (0.06)	3.0 (2.8)
<i>Polysiphonia fucoides</i>	+	–	–
<i>Ceramium nodulosum</i>	+	+	+
<i>Ceramium tenuicorne</i>	+	+	+
<i>Chondrus crispus</i>	–	–	0.1 (0.03)
<i>Corallina officinalis</i>	+	–	–
<i>Hildenbrandia</i> sp.	+	+	+
<i>Phymatolithon lenormandii</i>	+	+	+
Mean species richness	5.7 (1.1)	5.4 (0.5)	7.0 (1.2)
Mean total biomass	31 (7.7)	11 (1.3)	85 (27)

^aTotal biomass of Chlorophyta
^bTotal biomass of Phaeophyta, excluding crust-forming *Ralfsia verrucosa*
^cTotal biomass of Rhodophyta, excluding crust-forming *Hildenbrandia* sp. and *Phymatolithon lenormandii*

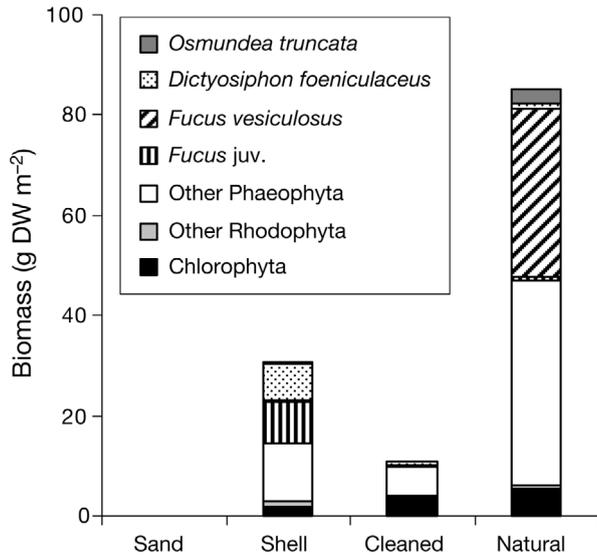


Fig. 3. Average biomass (g DW m⁻²) of different macroalgae groups and species (excluding crust-forming species) in different mussel treatments (n = 7): 'Sand', 'Shell', 'Cleaned', 'Natural'

was found in 'Natural', mainly due to the presence of large *Fucus vesiculosus* plants, which provided surfaces for attachment.

Macrofauna

A total number of 36 macrofauna species were observed (Table 4). Species richness differed significantly between the 'Sand' control and the mussel treatments ('Shell', 'Cleaned' and 'Natural') (ANOVA, $F_{3,22} = 58.63$, $p < 0.001$), but was not significantly different between mussel treatments (Fig. 4). In the 'Sand' control, a total of 8 species and on average 3.0 ± 0.3 (SE) species occurred, while in the mussel treatments the average species richness ranged between 18.1 and 19.1.

In the 'Sand' control, the dominant taxonomic groups were Gastropoda (*Hydrobia* sp.), which are typical for shallow sand bottoms in the region, while the dominant groups in the mussel treatments were Polychaeta and Crustacea, which are typical for hard and mixed substrate with algae and detritus. Crustacea comprised 11 species compared to 7 species for Polychaeta, but average abundance was higher in Polychaeta.

Average abundances were higher in patches with live mussels, although they differed statistically only from 'Sand' (ANOVA, $F_{3,22} = 7.50$, $p = 0.001$) and not from 'Shell' (Fig. 4). However, several differences in species composition were found among the mussel treatments. *Polydora ciliata* (ANOVA, $F_{2,18} = 12.62$, $p < 0.001$) and *Chironomidae* sp. (ANOVA, $F_{2,18} = 6.58$, $p =$

0.007) had significantly higher abundances in 'Shell' as compared to 'Cleaned' (SNK, n = 7, $p < 0.001$ and $p = 0.02$, respectively) and 'Natural' (SNK, n = 7, $p = 0.001$ and $p = 0.007$, respectively). *Ascidia conchilega* seemed to prefer dead shells for attachment. In addition, the sediment associated species *Corophium volutator* had high abundance in 'Shell' where they found surfaces to attach their tubes.

The abundance of *Balanus improvisus* differed significantly among the 3 mussel treatments (ANOVA, $F_{2,18} = 9.69$, $p = 0.001$) and was higher in 'Cleaned' (SNK, n = 7, $p = 0.01$) and 'Natural' (SNK, n = 7, $p = 0.001$) as compared to 'Shell'. The suspension feeders *Balanus improvisus*, *Spirorbis spirorbis*, *Cryptosula pallasiana* and *Metridium senile* were favoured in 'Cleaned', having higher abundance (SNK, n = 7, $p = 0.03$), which was significantly different from the other mussel treatments (ANOVA, $F_{2,18} = 3.97$, $p = 0.04$). No significant differences were found for the deposit feeders, although it had been expected that the increased biodeposition by mussels would yield a positive effect.

Algae-associated species such as *Psammechinus miliaris* were only present in 'Natural' where the algae biomass was high and where larger *Fucus vesiculosus* plants were present (Fig. 3). There was also high abundance of *Microdeutopus gryllotalpa* and other Crustacea, which find food and shelter in the algae. This complex community was also occupied by the common goby *Pomatoschistus minutus* and the *Mytilus* predator *Asterias rubens*. The average total biomass was significantly lower in 'Sand' than in the other treatments (ANOVA, $F_{3,22} = 6.05$, $p = 0.004$) (Table 5).

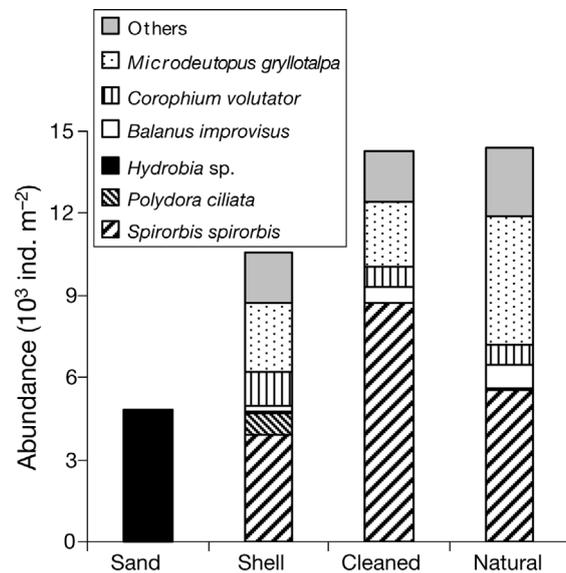


Fig. 4. Average abundance of dominant macrofauna species and 'others' for patches of different treatments (n = 7): 'Sand', 'Shell', 'Cleaned' and 'Natural'

Table 4. Average abundance of macrofauna (ind. m⁻² ± SE) for patches of different treatments: 'Sand', 'Shell', 'Cleaned' and 'Natural' (n = 7). Average number of taxa/species ± SE, total abundance (ind. m⁻² ± SE) and total biomass (g DW m⁻² ± SE) of macrofauna is also presented; -: taxon not present

Taxon	Sand		Shell		Cleaned		Natural	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Cnidaria								
<i>Metridium senile</i>	–		32	19	44	19	25	13
Oligochaeta								
<i>Tubificoides</i> sp.	5	5	25	25	19	19	6	6
Polychaeta (total)	25	25	5010	1056	8914	1491	5937	1403
<i>Eulalia viridis</i>	–		6	6	13	13	–	
Phyllodocidae	–		19	13	25	19	38	26
<i>Nereimyra punctata</i>	–		–		–		32	25
Nereidae	–		102	27	25	13	108	37
<i>Harmothoe imbricata</i>	–		70	21	121	30	152	55
<i>Polydora ciliata</i>	–		806	353	19	9	44	32
<i>Spirorbis spirorbis</i>	–		3879	1302	8698	1466	5549	1371
Other	25	25	126	84	13	8	13	8
Gastropoda (total)	4772	476	368	56	311	121	241	51
<i>Bittium reticulatum</i>	10	10	25	19	–		–	
<i>Nassarius reticulatus</i>	5	5	25	19	25	19	25	9
<i>Hydrobia</i> sp.	4747	477	63	25	13	13	25	13
<i>Littorina littorea</i>	–		146	29	127	34	121	36
<i>Lepidochitona cinerea</i>	–		44	14	19	9	51	18
<i>Rissoa</i> sp.	10	6	63	32	127	113	19	13
Bivalvia (total)	20	9	153	44	154	23	184	80
<i>Cerastoderma</i> sp.	15	6	51	18	51	20	89	42
<i>Mya arenaria</i>	5	5	102	35	102	25	95	23
<i>Spisula truncata</i>	–		–		–		13	13
Cheliceriformes								
Halacaridae	–		–		6	6	–	
Crustacea (total)	–		4451	998	4273	745	7149	1502
<i>Athanas nitescens</i>	–		6	6	–		–	
<i>Balanus improvisus</i>	–		184	75	559	150	876	130
<i>Carcinus maenas</i>	–		197	56	152	32	178	44
<i>Corophium volutator</i>	–		1301	374	781	224	724	245
<i>Crangon crangon</i>	–		–		–		6	6
<i>Microdeutopus gryllotalpa</i>	–		2470	543	2356	455	4705	1296
Amphipoda juv.	–		254	76	381	123	597	256
<i>Palaemon elegans</i>	–		32	25	44	31	63	43
<i>Callinectes</i> sp.	–		6	6	–		–	
Bryozoa								
<i>Cryptosula pallasiana</i> (No. of colonies)	–		248	93	330	115	667	168
Echinodermata								
Asterioidae	–		13	8	57	13	70	23
<i>Psammechinus miliaris</i>	–		–		–		6	6
Chordata								
<i>Ascidia conchilega</i>	–		32	18	13	13	–	
Vertebrata								
<i>Pomatoschistus minutus</i>	–		6	6	6	6	51	12
Insecta								
Chironomidae sp.	–		70	21	19	9	6	6
Other	–		–		6	6	–	
Mean total abundance	4822	477	10408	1913	14152	1452	14356	2205
Mean number of taxa	3.0	0.3	19.1	1.6	18.1	1.1	18.6	1.3
Mean total biomass	15	5	86	37	65	17	73	12

Table 5. Summary of various studied parameters (n = 5) of the role of *Mytilus* structural properties and biological activities for biodiversity of associated communities. Values are mean (±SE). Species richness refers to total in patch (i.e. per 225 cm²)

Parameter	Sand	Shell	Cleaned	Natural
Macrofauna				
Species richness	3.0 (0.3)	19.1 (1.6)	18.1 (1.1)	18.6 (1.3)
Abundance (10 ³ ind. m ⁻²)	4.8 (0.5)	10.4 (1.9)	14.2 (1.5)	14.4 (2.2)
Biomass (g DW m ⁻²)	15 (5)	86 (37)	65 (17)	73 (12)
Macroalgae				
Species richness	0	5.7 (1.1)	5.4 (0.5)	7.0 (1.2)
Biomass (g DW m ⁻²)	0	31 (7.7)	11 (1.3)	85 (27)
Sediment				
C content (%)	0.25 (0.01)	0.29 (0.02)	0.36 (0.04)	0.39 (0.04)
N content (%)	0.03 (0.001)	0.04 (0.002)	0.05 (0.005)	0.05 (0.005)
Metabolism				
GP/R 24 h	1.82 (0.14)	1.02 (0.11)	0.69 (0.09)	0.74 (0.08)

NP since there was growth of some larger *F. vesiculosus* and filamentous Phaeophyta. Respiration (R) was lowest in the 'Sand' community with low animal and plant biomass. In the 'Shell' community, respiration was rather high, probably due to a fairly high biomass of algae (*F. vesiculosus* germlings and *Dictyosiphon foeniculaceus*) and the activity of associated fauna, including some larger individuals of *Carcinus maenas* and *Palaemon* sp. in some samples. The observed respiration of 'Cleaned' and 'Natural' were higher than 'Sand', which was due to more associated fauna and microbial activity in sediments enriched by mussel biodeposits, especially in the 'Natural' community.

Sediment

Total carbon and nitrogen contents of the sediment ranged from 0.22 to 0.57% for carbon and 0.03 to 0.08% for nitrogen (Table 5). The carbon content differed significantly among treatments (ANOVA, $F_{3,22} = 6.69$, $p = 0.002$). The 'Sand' control was significantly lower than in 'Cleaned' (SNK, $n = 7$, $p = 0.03$) and 'Natural' (SNK, $n = 7$, $p = 0.002$). There was also a significant difference between 'Shell' and 'Natural' (SNK, $n = 7$, $p = 0.014$). Significant differences among treatments were also seen for nitrogen content of the sediment (ANOVA, $F_{3,22} = 6.05$, $p = 0.004$), with 'Sand' significantly lower than 'Cleaned' (SNK, $n = 7$, $p = 0.03$) and 'Natural' (SNK, $n = 7$, $p = 0.004$). In addition, 'Shell' was significantly different from 'Natural' (SNK, $n = 7$, $p = 0.02$). The C/N ratio ranged between 7.4 and 8.5, but did not differ among treatments.

Community metabolism

Fig. 5 shows the community metabolism parameters of associated benthic fauna and flora (macroscopic and microscopic) as well as plankton and bacteria in the 'Shell', 'Cleaned' and 'Natural' communities after correction for respiration of mussels and metabolism of the 'Sand' community outside mussel patches.

Net production (NP) was highest in the 'Sand' and 'Shell' communities due to microalgae films on the sediment and growth of newly settled *Fucus vesiculosus* germlings as well as *Dictyosiphon foeniculaceus* on the mussel shells. NP was lowest in the community that had been 'Cleaned' from associated fauna and flora 3 mo earlier. The 'Natural' patch also has fairly high

Gross production (GP) was highest in the 'Shell' and 'Natural' communities, which had the highest growth of macroalgae. 'Sand' and 'Shell' had the highest GP/R ratio and were thus the most self-supporting communities. For all communities, the GP/R ratio exceeded 1 over a 3 h period at midday. If calculated over 24 h (12 h light and 12 h dark), GP/R ratios were 1.8 for the 'Sand' and 1.0 for the 'Shell' communities respectively, indicating that these were energetically self supporting during the time of the study, whereas the 'Cleaned' and 'Natural' communities had GP/R ratios of 0.7 and 0.8 respectively, indicating that they need a net import of energy in order to satisfy their energy demands.

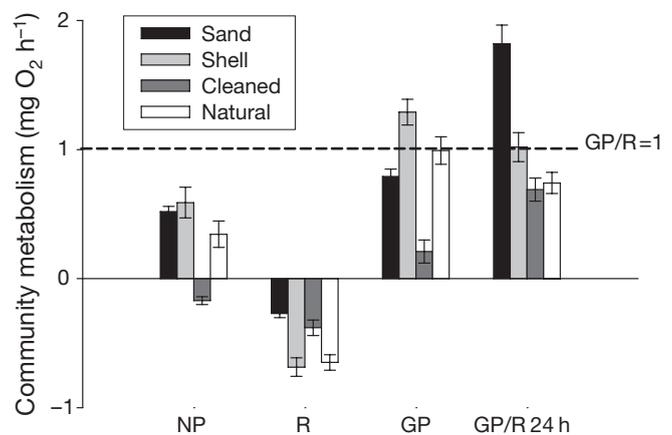


Fig. 5. Calculated community metabolism (mg O₂ h⁻¹) of associated fauna, flora and microbes, corrected for mussel respiration and metabolism of sand community area surrounding the patches. Parameters for 'Sand' not corrected. NP: net production, R: respiration, GP: gross production, GP/R: ratio of gross production to respiration. Dashed horizontal line: GP/R 24 h = 1. Error bars: ±SE

Relative role of structure and function

The relative roles of physical structure and mussel biology and activity in terms of the biodiversity, biomass and function of the associated fauna and flora and the mussel community at the study site is summarized in Table 5.

A comparison of the 'Sand' control and empty 'Shell' patches, where the number of fauna taxa increased from 1.2 to 19.1 and flora from 0 to 5.7 respectively, clearly shows that the most important factor for macrofauna and -flora biodiversity is the structure created by shells. The presence of live mussels in 'Cleaned' and 'Natural' did not lead to any additional increase in total number of taxa, although there were some changes in species composition, as some species are favoured and some species are disadvantaged by the presence of live mussels. The abundance of macrofauna also peaked in these treatments.

DISCUSSION

Facilitation effects on biodiversity of associated species

The present study aimed at identifying and separating the effects of the physical structure of the mussel patch from the effects of the biological activity of live mussels on the diversity and composition of associated species as well as on community metabolism and production. The comparisons among the adjacent sand flat, empty shells, cleaned mussels, and natural patches of different sizes clearly demonstrated the habitat-modifying ability of *Mytilus edulis* in terms of differences in species richness, abundance and composition, as well as altered organic content in sediment and ecosystem functioning. After 3 mo colonisation, the species richness of macroalgae and macrofauna was about the same in the 'Shell' and 'Cleaned' mussel treatments and approached that of the 'Natural' patches. This indicates that the physical structural properties of the mussels are the main factor controlling the biodiversity of associated species. The proposed mechanism for this is that the structure serves as surface for attachment of fauna and flora, traps detritus and also provides refuge and shelter for some species through the increased habitat complexity (Suchanek 1985, Yager et al. 1993, Albrecht 1998).

However, the average macrofauna abundance in 'Cleaned' and 'Natural' was higher than in 'Shell', indicating that the biological activities of the mussels have an additional positive effect on the total abundance of macrofauna. This is probably due to the increased supply of mussel biodeposits as a food source, which was expressed as increased levels of organic carbon and nitrogen in the sediment.

These results for macrofauna are largely supported by earlier attempts to discriminate between the role of structure and function for biodiversity in various mussel communities (e.g. Crooks & Khim 1999, Ragnarsson & Raffaelli 1999). Previous studies indicate that species richness is dependent on whether mussels are situated on rocky shores or sediment bottoms (Thiel & Ullrich 2002), and is probably related to whether mussel faeces are biodeposited and continuously accumulated in the mussel bed, or if they are washed away by waves and currents. Biodiversity effects are also certainly dependent on spatial scale and patch arrangement as well as mussel patch size (Hewitt et al. 2002, Norkko et al. 2006).

For macroalgae the pattern seems more complex and biological interactions and function seem to play a larger role.

Role of structure

Both the structural and biological traits of the mussels contributed to the abundance and composition of associated organisms. Our study showed that *Balanus improvisus*, *Spirorbis spirorbis*, *Littorina littorea*, encrusting algae (e.g. *Ralfsia verrucosa* and *Phymatolithon lenormandii*) and macroalgae, such as brown algae (*Dictyosiphon foeniculaceus* and *Fucus vesiculosus*) are favoured by the availability of hard substratum. The shell structure specifically favoured *Polydora ciliata* and *Ascidia conchilega* as well as Chironomidae and *Corophium volutator*. The shells also provided substratum for the growth of *Fucus* spp. and the secondary association of fauna and flora linked to this 'engineering species'. The presence of shells also influences the benthic boundary layer by creating micro-turbulence (Frechette et al. 1989) and physically trapping drifting detritus (Yager et al. 1993), as evidenced by the observed increase in sediment organic and nutrient contents also in the 'Shell' treatment without live mussels present. Some of this is probably also due to faeces from associated fauna that accumulated within the patches.

Role of function and species interactions

These structural and functional traits are conducive to colonisation by many species, but some seem to be specifically affected by the biological activity of mussels. Some species have a more or less commensal relationship with mussels, e.g. sessile suspension feeders like *Balanus improvisus*, *Spirorbis spirorbis* and *Cryptosula pallasiana*, which can successfully settle on live mussels mainly because the mussels keep competitors

away, and which will benefit from the filtration currents generated by *Mytilus edulis* (Laihonen & Furman 1986). For other invertebrate species, the filtration activity of *M. edulis* has been shown to inhibit larvae settlement (Cowden et al. 1984).

For macroalgae, we found both positive and negative interactions with *Mytilus edulis*. Thus, total biomass of algae in patches of 'Cleaned' live mussels was only one third of that in patches of empty 'Shells'. This was probably due to the ability of *M. edulis* to actively filter larvae and algal spores from the water (Santelices & Martinez 1988) and to clean its shell from fouling organisms such as small *Fucus* spp. and *Dictyosiphon foeniculaceus* germlings by use of its prehensile foot (Theisen 1972), thereby inhibiting recruitment. In contrast, a positive effect was found for fast growing Chlorophyta (i.e. *Ulva* sp.) that occurred mainly on live mussels, perhaps facilitated by *M. edulis* providing the algae with nutrients. Furthermore, green algae seem to grow better when mussels inhibited the recruitment of competing *Fucus vesiculosus* (Albrecht 1998). However, only single *F. vesiculosus* germlings need to survive in order to result in the high *F. vesiculosus* biomass and complex association found in the large patches and the 'Natural' community.

Role of biological processes

Community metabolism (GP/R ratio) (Odum 1969) integrates all changes in oxygen due to production by all primary producers present (plankton, macro- and microalgae) as well as their respiration and that of macro- and meiofauna, bacteria and other microorganisms; it is therefore a good indicator of biological activity and energy flow in the community. The GP/R ratio declined from the 'Sand' control through 'Shells' to the communities with live mussels ('Cleaned' and 'Natural') due to increasing biomass, and thus, also respiration of flora and fauna, as well as respiration of bacteria associated with increasing amounts of biodeposits and accumulated organic matter. The GP/R^{24h} ratios of 1.8 for the 'Sand' and 1.0 for the 'Shell' communities, respectively, indicate that these were energetically self supporting during the time of the study, whereas the 'Cleaned' and 'Natural' communities, with GP/R^{24h} ratios of 0.56 and 0.76 respectively, need a net import of energy corresponding to at least 44 and 24 %, respectively, of the total energy demand of the associated communities (cf. Hopkinson & Smith 2004). This demand would essentially be covered in the form of particulate organic matter that is filtered from the water column and biodeposited by the mussels. The presence of larger *Fucus vesiculosus* plants in 'Natural' may explain the somewhat lower deficit

compared to 'Cleaned' because in addition to structure, it also provides benthic primary production for grazers.

Effects of patch size on community structure

Our results suggest that when a sandy bottom is colonised by living mussels and their resulting empty shells, considerable increases in associated species can be observed. Clear relationships with patch size were found for fauna and flora diversity up to a saturation level at about 125 cm² for naturally occurring mussel patches. Above this level, species composition and the biomass of macrofauna and -flora were probably also secondarily dependent on the biomass of *Fucus vesiculosus*, which adds a further 3-dimensional structure to the patch. Thus, *F. vesiculosus* should probably be regarded as an engineering species on its own, adding complexity and providing substrate for fauna and flora as well as shelter against predation and physical stress (Albrecht & Reise 1994). While no macroalgae at all were found outside mussel patches, both the number of algal taxa and biomass increased with patch size. The high species richness of macroalgae observed in large patch sizes was mainly due to the facilitation effects of fucooids on epiphytic alga species, such as *Spermatochneus paradoxus*, *Elachista fucicola*, *Pilayella littoralis*, *Ectocarpus siliculosus* and *Polysiphonia fucoides*, and on epiphytic invertebrates, i.e. *Dynamena pumila* and *Electra pilosa*. Some of these (e.g. *E. fucicola* and *D. pumila*) are specifically associated with fucooids and would not occur without the host species. Other algae-associated species such as *Psammechinus miliaris* were only present in 'Natural', where the algae biomass was high and larger *F. vesiculosus* plants were present. There was also high abundance of *Microdeutopus gryllotalpa* and other Crustacea, which find food and shelter in the algae (cf. Arrontes 1999). Albrecht & Reise (1994) showed that macroalgal cover with *F. vesiculosus* changes the surface properties of mussel beds, negatively affecting the mussel density and epibionts, but supporting various herbivores and increasing overall benthic diversity.

The macrofauna assemblage associated with *Mytilus edulis* was dominated by Crustacea, Gastropoda and Polychaeta, and the patches showed highly favourable conditions for a variety of functional groups, i.e. suspension feeders (e.g. *Balanus improvisus*, *Spirorbis spirorbis*), deposit feeders (e.g. *Rissoa* sp. and *Hydrobia* sp.) and herbivores (e.g. *Microdeutopus gryllotalpa*, *Littorina littorea*), all of which tended to increase in abundance with increasing patch size.

Organic matter (C and N) increased in the sediment with increasing patch size due to the biodeposition by



M. edulis and to the physical ability of spaces to trap sediments and drifting detritus (Yager et al. 1993). For this process, the assumption that large patches are older would also be somewhat important, as older patches would accumulate organic matter over a longer time. High organic content should be beneficial to deposit-feeding organisms (cf. Commito 1987, Dittmann 1990, Ragnarsson & Raffaelli 1999); however, though we found more deposit feeders in large patches, the differences were not significant.

CONCLUSIONS

We conclude that the species richness of mussel communities is almost entirely controlled by structural properties, with species composition being modified through biological interactions with mussels. In contrast, the biological activities of mussels (i.e. biodeposition, nutrient recycling and water clearance) seem, to a large extent, to determine carrying capacity (i.e. abundance, biomass) and community functioning.

We also conclude that the mussel-associated communities depend on energy resources supplied by imports from the pelagic system through mussel filtration. Consequently, there is a shift from a largely primary producer- and grazer-dominated food chain in the 'Sand' and 'Shell' communities of associated fauna and flora to a more detritus-based food chain when live mussels are present. The detritus-based food chain is largely dependent on the activity of mussels in removing plankton and nutritious organic particles from the pelagic and depositing them on the sea floor.

Whereas structural properties determine biodiversity of the associated community, we emphasize the importance of functional traits as the basis for sustaining the community. Community metabolism was a good indicator of ecosystem functioning and an important parameter for understanding energy flow and sustainability of the system.

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