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Comparing biodiversity effects among ecosystem engineers of contrasting strength: macrofauna diversity in *Zostera noltii* and *Spartina anglica* vegetations

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Abstract Whereas it is well known that ecosystem engineers can have a large influence on biodiversity, underlying mechanisms are still not fully clear. We try to enhance insight by comparing biodiversity effects of two neighboring intertidal, clonal, ecosystem engineering plant species that modify the physical environmental parameters in a similar way, but with a different magnitude. Macrobenthic assemblages were compared between meadows of the seagrass *Zostera noltii*, small patches (≤ 0.5 m Ø) and large areas ($\gg 5$ m Ø) of the emergent halophyte *Spartina anglica* and the surrounding bare tidal mudflat (control). Multivariate analyses revealed that the mudflat benthic assemblage and *Zostera* meadow assemblage showed highest similarities, whereas the *Spartina* marsh assemblage showed the highest dissimilarity with these two areas. Whereas the descriptive nature of our study limits interpretation of the data, some clear patterns were observed. For all vegetated areas, species diversity was lower compared to the unvegetated mudflat, and we observed a strong shift from endo- towards epibenthic species, suggesting that increased above-ground habitat complexity may be a main driving process in our system. As there were no clear patterns related to feeding types, food availability/productivity appeared to be of minor importance in structuring the benthic assemblages. Nevertheless, animals were in general smaller in vegetated areas. Patchiness had a distinct positive effect on biodiversity.

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Introduction

Since the introduction of the concept of ecosystem engineers as organisms that cause a large and/or distinct modification of the abiotic environment (Jones et al. 1994, 1997), it has been well recognized that ecosystem engineers can have a large influence on biodiversity within a specific habitat (e.g., see Crooks 2002; Wright and Jones 2004, 2006). For example, ecosystem engineers may enhance diversity by facilitating the presence of other organisms or communities (e.g., Bruno et al. 2003) which may eventually lead to succession (e.g., Castellanos et al. 1994; Fogel et al. 2004). Engineering species may also enhance diversity by causing spatial or temporal heterogeneity (e.g., excavations by pocket gophers, Reichman and Seabloom 2002; fungus-growing termites, Jouquet et al. 2004). On the other hand, the physical alteration of ecosystems by invasive ecosystem engineers can have cascading effects on many resident species (Crooks 2002). Despite the well-recognized importance of ecosystem engineering for biodiversity, we lack fundamental understanding of how ecosystem engineers affect biodiversity and we are not yet able to predict the type of ecosystems in which engineers are most critical for biodiversity (Jones et al. 1997). Some broad generalizations can, however, be made in terms of ecosystem engineering effects on biodiversity via habitat complexity, productivity and spatial scale.

Engineers that increase habitat complexity tend to increase the diversity and/or the abundance of organisms

(Crooks 2002). This is often the case for autogenic engineers that modify the habitat via their own physical structure (e.g., trees in a forest). Allogenic engineers that modify the environment by transforming living or non living materials from one state to another (e.g., beavers), often reduce habitat complexity and thereby biodiversity (Crooks 2002). Wright and Jones (2004) proposed that the diversity effect of an ecosystem engineer depend on the relationship between biodiversity and productivity. Ecosystems where biodiversity is restricted by a too low productivity would increase in diversity if the engineer enhances productivity, and vice versa. Similarly, ecosystems where biodiversity is restricted by a too high productivity would increase in diversity if the engineer reduces productivity, and vice versa (Wright and Jones 2004). In addition to effects on diversity by ecosystem engineers via modification of the habitat complexity and/or productivity, diversity effects also depend on spatial scale. At larger scales, the effects are commonly positive when comparing engineered and un-engineered environments (Jones et al. 1997; Wright and Jones 2004).

One of the main challenges in obtaining in depth understanding of the effects of ecosystem engineering on biodiversity is to detangle the effects due to a changed productivity versus due to a changed habitat complexity. A possible way to achieve this might be the comparison of effects on biodiversity by ecosystem engineers that modify the physical environmental parameters in a similar way, but differ in the magnitude that they modify the environment. In this study, we apply this approach by comparing the diversity effect of two well known neighboring ecosystem engineering clonal plant species that inhabit the intertidal transition zone between the bare tidal mudflat and the vegetated salt marsh: the seagrass *Zostera noltii* and the emergent halophyte *Spartina anglica*. Apart from their contrasting ecosystem engineering strength, this species selection is relevant because *Spartina* species invade tidal flats in many places in the world, thereby taking over bare mudflat as well as *Zostera* habitats (Lacambra et al. 2004; Wang et al. 2006; Cottet et al. 2007). Because of the latter, there is considerable concern about the impact of *Spartina* on benthic macrofauna and thereby birds that feed on these animals. Apart from a shift in benthic assemblages, birds may also not able to physically reach benthos living in the marsh vegetation. Researchers studying invasive *Spartina* have reported altered faunal composition and abundance (e.g., Hedge and Kriwoken 2000; Neira et al. 2005) and trophic function (Levin et al. 2006).

The seagrass *Z. noltii* and the emergent halophyte *S. anglica* differ in the extent that they modify their environment. Both species strongly enhance the habitat complexity by making shoots that protrude as physical structures on the mudflat. The vegetation of *Z. noltii* is most dense (Bouma et al. 2005), with the flexible shoots lying on the sediment surface at low tide. *Spartina anglica* is characterized by much taller and stiffer shoots and a larger above-ground biomass. Positive habitat complexity effects of *Spartina* on benthic assemblages may be counteracted by its effect on sediment properties, as *Spartina* forms well-defined dome-shaped tussocks (Castellanos et al. 1994; Bouma et al. 2007; van Hulzen et al. 2007) with a relatively compact, densely rooted, well aerated, dry sediment (Van Wesenbeeck et al. 2007). This effect on sediment properties may be expected to be more pronounced in mature *Spartina* marshes than in more recently established *Spartina* tussocks, as the latter will contain a lower shoot and root density.

Both *Zostera* and *Spartina* have been shown to enhance particle and sediment accretion by reduction of hydrodynamic energy in a complex way (for seagrasses see, e.g., Orth 1992; Bologna and Heck 2002; Widdows and Brinsley 2002; Blanchet et al. 2004; for *Spartina* see, e.g., Kneib 1984; Netto and Lana 1997; Widdows and Brinsley 2002). As the shoots of *S. anglica* are much stiffer and taller than the flexible shoots of *Z. noltii*, *Spartina* causes a much stronger attenuation of wave energy than *Zostera* (Bouma et al. 2005). Such reduction of hydrodynamic energy may lead to an enhanced accretion of organic materials and thereby an enhanced food supply to benthic animals that live from deposited debris (e.g., surface deposit feeders, grazers). However, because of the lower density of the *Spartina* than *Zostera* vegetation, *Spartina* maintains a higher canopy flux under unidirectional flow (Peralta et al. 2008). Such flux through the canopy is needed both to provide food supply to benthic animals that live inside vegetations and depend on water refreshment for their food supply (e.g., filter feeders; Brun et al., this issue) and to provide materials to maintain high rates of accretion within the vegetated areas (Peralta et al. 2008).

Based on the hydrodynamic and sediment engineering properties of both plant species, we hypothesize that (1) *Spartina* vegetated sediments will have finer sediment grain size and a higher organic matter content, and a reduced microalgal chlorophyll *a* biomass relative to the adjacent unvegetated tidal flat sediments, with *Zostera* vegetations taking an intermediate position, and (2) that these differences cause changes in the benthic macrofauna assemblage structure and functional groups. That is, we expect that (2a) enhanced accretion of organic matter in vegetations may benefit the occurrence and diversity of deposit feeders, and that (2b) the reduced hydrodynamic energy in vegetations will reduce overall food supply to filter feeders and thereby their occurrence and diversity. Based on the habitat complexity engineering properties of both plant species we furthermore hypothesize that (3) both plant species will cause a shift from endobenthic to

epibenthic macroinvertebrate species, as the vegetation provides habitat and protects the epibenthic animals from predation. Based on the sediment engineering properties of both species, we predict this shift to be most pronounced in the *Spartina* vegetation, because of sediment compaction and sediment aeration. Finally, we hypothesize that (4) smaller and generally younger patches of *Spartina* support a more diverse benthic macrofaunal assemblage compared to larger and generally more mature *Spartina* patches, due to a stronger change in the sedimentary environment in the latter.

We tried to evaluate our hypotheses by determining the epi- and endobenthic macrofaunal diversity (i.e., species composition, functional groups by feeding types, abundance, biomass) in the seagrass *Z. noltii*, the emergent macrophyte *S. anglica* and in the adjacent bare, unvegetated mudflat. We focused on macrofaunal assemblages because it represents an important trophic link between primary producers and higher consumers such as birds and fishes. We estimated the vegetation effects on habitat complexity by counting the shoot density and estimating above- and below-ground biomass. We estimated accretion of organic debris by looking at the organic carbon content and the mud content, as mud is trapped along with organic debris. Since the attenuation of hydrodynamic energy is a spatial explicit process (e.g., see Bouma et al. 2005, 2007), we assessed the importance of scale by comparing small *Spartina* tussocks (≤0.5 m Ø) and large patches of *Spartina* marsh (>5.0 m Ø).

Materials and methods

Study area

The study was conducted at the transition from the tidal flat to the salt marsh at Ritthem (51°27N, 03°39E) at the mouth of the Westerschelde estuary, in the south-west of the Netherlands (Fig. 1). Ritthem is an embayment marsh that is protected by an extensive breakwater that was built in 1965 in connection with the Sloehaven harbor development, close to the harbor of the city of Vlissingen (Dyer et al. 2002). Nearby Ritthem, the mean vertical tidal range is 3.8 m and salinity is about 29 (Ysebaert et al. 2003). The transition from the tidal flat to the salt marsh is dominated by two plant species that grow very close to each other: the emergent macrophyte *S. anglica* and the seagrass species *Z. noltii*. The transition zone from mudflat to salt marsh has a gentle slope and no cliff occurred at the study site.

Experimental design

Within the transition zone from bare to vegetated, four distinct sampling habitats were distinguished: (i) bare mudflat, (ii) *Zostera* meadow, (iii) *Spartina* marsh vegetation (i.e., large patches, >5.0 m Ø) and (iv) small *Spartina* tussocks (i.e., ≤0.5 m Ø). In the first three habitats, five locations were selected to obtain a block design. At each location three replicate sample sites were randomly chosen (Fig. 1). Unfortunately, it was not possible to find small *Spartina* tussocks located in such way that they could match the block design. Hence, 15 small tussocks were selected randomly. Each of these small tussocks was used as a single sample, as sampling would often mean that the whole tussock was lost. Sampling took place in the period where both the plant biomass and macrofaunal biomass has reached a maximum (i.e., 14th September and 4th October 2004).

Sampling

At each sampling point a frame of 1 m² was placed over the vegetation or on the sediment. In case of the small, recently established *Spartina* tussocks (i.e., ≤0.5 m Ø), the whole tussock was sampled and regarded as the sampling surface. Within this area, the number of stems and all visible worm piles of the lugworm *Arenicola marina* were counted. Subsequently, all vegetation and large epibenthos (i.e., the ones that are visible on the surface) were collected. The epibenthos was stored in buffered formaldehyde (4%). The top centimeter of the sediment was collected with a syringe (Ø 10 mm) for grain size analysis and chlorophyll analysis. For each analysis three samples were collected randomly, lumped and immediately stored cooled in the dark. A core with a diameter of 110 mm was pushed 300 mm deep into the sediment to sample benthos. The core samples were stored in plastic bags until washing at the laboratory.

In the laboratory, the vegetation collected in the 1 m² frames was washed carefully to remove sediment and to collect any macrobenthos attached to the vegetation. The macrobenthos was added to the epibenthic sample collected in the field. For each location, twenty stems of *S. anglica* and *Z. noltii* were used to measure the total length of the stem, the height where leaves branch off and leaf length. The 20 measured stems were dried separately from the others stems. All vegetation samples were dried at 80°C for 2–4 days, and subsequently weighed. After washing the sediment sample over a 1 mm mesh sieve, the endobenthos samples were stored in buffered formaldehyde (4%) for later analysis.

Fig. 1 Schematic
representation of the benthos
sampling at our field site. *Top
left* position of the study site in
the southwestern part of The
Netherlands. *Top right* Ritthem
salt marsh at the mouth of the
Westerschelde estuary. *Bottom
figure* study site with position of
the different sampling points in
each of the four habitats. For
detailed information about the
sampling design: see text. The
aerial picture underneath the
sampling points is from a
different year, so that samples
taken in the vegetation
(indicated in *red*) may appear to
fall outside of the vegetation
(color in online)
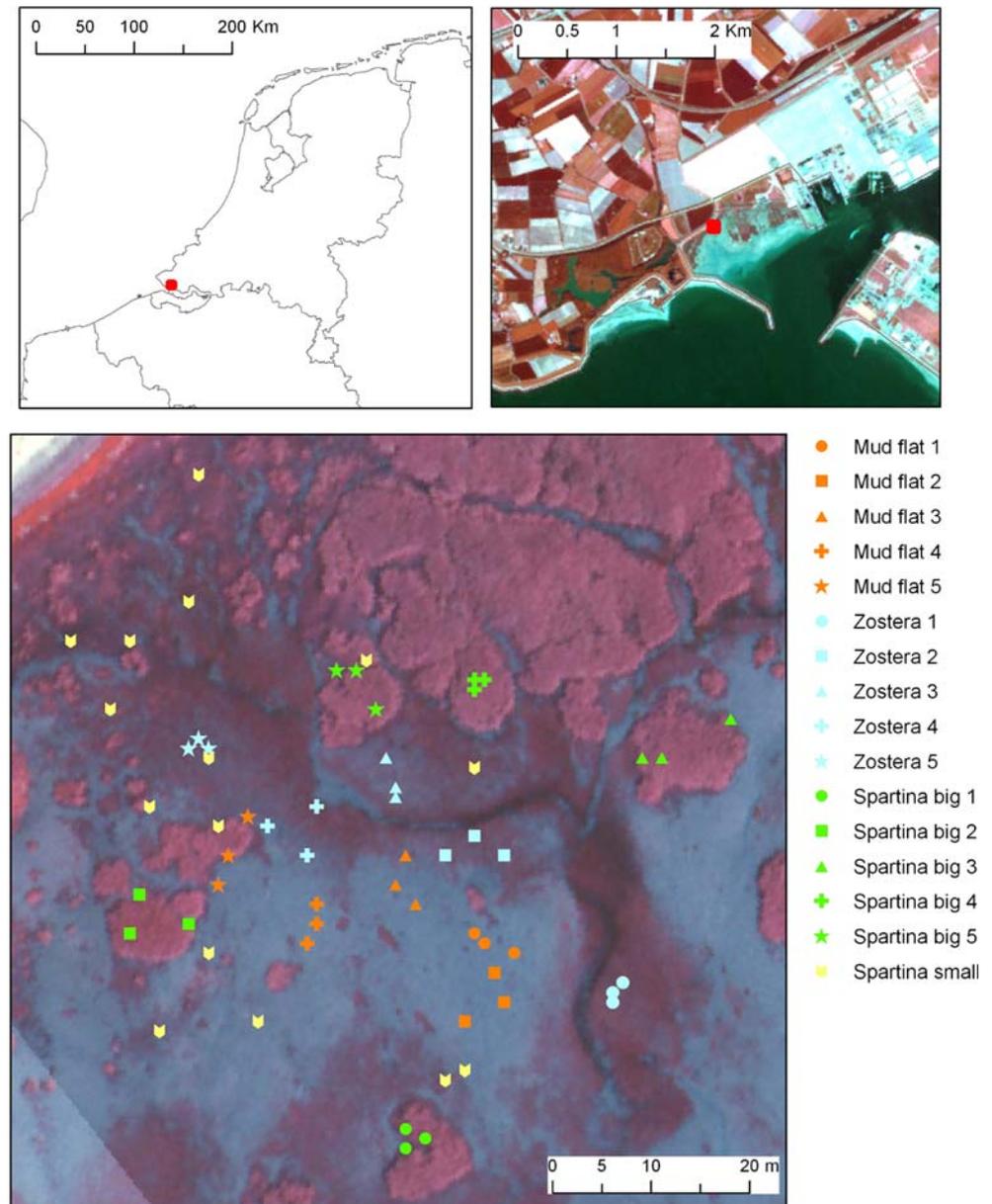
Analyzing epi- and endobenthos

Epifauna is defined as those animals that live on top of the
sediment or are attached to structures above the sediment,
and which spend most of their feeding activity on top of the
benthic surface. Animals that spend most of their lives
digging and burrowing in soft sediments are referred to as
endofauna (infauna).

After staining the benthos with Rose Bengal, organisms
were identified to species level (except for Nemertea, Ol-
igochaeta, Chaetognata, Nudibranchia and Actiniaria),
counted and weighted. Since Annelids were often broken
due to handling, only parts with a head structure were
counted. The length of bivalves and some gastropods

(*Macoma balthica*, *Cerastoderma edule*, *Mytilus edulis*,
Littorina littorea) and crustaceans (*Carcinus maenas*) were
measured to the nearest mm.

All species were grouped in taxonomic classes and
functional groups based on the feeding type. We distin-
guished five functional groups (Table 1): (1) suspension
feeders (SF) that filter water to collect their food, mainly
phytoplankton (e.g., *C. edule*, *Actiniaria*); (2) surface
deposit feeders (SDF) that typically feed on diatoms on the
surface of the sediment (e.g., *M. balthica*, *Tharyx marioni*).
This group also includes grazers that graze on microalgae
on the sediment surface or vegetation (e.g., *Hydrobia
ulvae*); (3) sub-surface deposit feeders (SSDF) that pre-
dominantly feed on micro-organisms, phytobenthos and

Table 1 Mean densities and biomass of macrofauna in the four habitats

Species	Feed		Mud flat		Zostera meadow		Spartina patch		Spartina marsh	
			Abundance ind m^{-2}	Biomass g AFDW m^{-2}	Abundance ind m^{-2}	Biomass g AFDW m^{-2}	Abundance ind m^{-2}	Biomass g AFDW m^{-2}	Abundance ind m^{-2}	Biomass g AFDW m^{-2}
Annelida, Polychaeta										
Anaitides mucosa	P	Endo	0	0	21 ± 15	0.017 ± 0.013	7.0 ± 7.0	0.009 ± 0.009	0	0
Arenicola marina	SSDF	Endo	112 ± 19.1	5.1 ± 1.5	77 ± 21	0.934 ± 0.384	42 ± 14	2.792 ± 1.455	0	0
Boccardiella ligerica	?	Endo	0	0	0	0	7.0 ± 7.0	0.009 ± 0.009	0	0
Capitella capitata	SSDF	Endo	154 ± 38.2	0.03 ± 0.011	28 ± 38	0.002 ± 0.001	49 ± 23	0.011 ± 0.008	0	0
Eteone sp.	P	Endo	49 ± 17.4	0.048 ± 0.022	98 ± 17	0.068 ± 0.016	0	0	0	0
Glycera tridactyla	P	Endo	0	0	0	0	7.0 ± 7.0	0	0	0
Heteromastus filiformis	SSDF	Endo	1,978 ± 261.4	2.7 ± 0.3	2,974 ± 243	3.152 ± 0.305	2,939 ± 637	4.271 ± 0.681	330 ± 70	0.192 ± 0.079
Malacoceros sp.	SDF	Endo	246 ± 104.1	0.015 ± 0.007	252 ± 145	0.018 ± 0.010	112 ± 33	0.015 ± 0.005	0	0
Micropthalmus sp.	SDF	Endo	0	0	0	0	14 ± 7	0	0	0
Micropthalmus sczelkowii	SDF	Endo	0	0	0	0	0	0	7.0 ± 7.0	0
Nephtys Caeca	O	Endo	7.0 ± 7.0	0.034 ± 0.034	0	0	0	0	0	0
Nephtys hombergii	P	Endo	14 ± 9.6	0.063 ± 0.044	7.0 ± 7.0	0.244 ± 0.244	0	0	0	0
Nereis sp.	O	Endo	28 ± 12.4	0.026 ± 0.021	0	0.000	0	0	0	0
Nereis diversicolor	O	Endo	14 ± 9.6	0.004 ± 0.003	7.0 ± 7.0	0.000	28 ± 12	0.052 ± 0.051	28 ± 12	0.008 ± 0.007
Polydora ligni	SF	Endo	7.0 ± 7.0	0.006 ± 0.006	119 ± 64	0.010 ± 0.006	0	0	0	0
Pygospio elegans	SDF	Endo	1,585 ± 530.4	0.619 ± 0.526	2,062 ± 535	0.153 ± 0.023	196 ± 72	0.019 ± 0.008	0	0
Scololepis foliosa	P	Endo	7.0 ± 7.0	0.311 ± 0.311	0	0	0	0	0	0
Streblospio shrubsolii	SDF	Endo	70 ± 35.1	0.003 ± 0.002	63 ± 41	0.003 ± 0.002	35 ± 20	0.002 ± 0.001	0	0
Tharyx marioni	SDF	Endo	182 ± 58.5	0.007 ± 0.002	989 ± 25	0.102 ± 0.026	84 ± 31	0.006 ± 0.002	0	0
Polychaeta unident	?	Endo	0	0	0	0	0	0	7.0	0.001 ± 0.001
Annelida, Oligochaeta										
Oligochaeta	SSDF	Endo	2,841 ± 745.9	0.401 ± 0.093	2,273 ± 770	0.402 ± 0.106	9,688 ± 1,967	1.8 ± 0.5	4,441 ± 921	0.53 ± 0.12
Chaetognatha										
Chaetognatha	P	Endo	0	0	7.0 ± 7.0	0	0	0	0	0
Nemertea										
Nemertea	P	Endo	7.0 ± 7.0	0.007 ± 0.007	21 ± 11	0.007 ± 0.004	253 ± 138	0.41 ± 0.28	42 ± 29	0.009 ± 0.007
Mollusca, Bivalvia										
Cerastoderma edule	SF	Endo	133 ± 31.6	4.1 ± 1.8	77 ± 36	1.274 ± 0.975	154 ± 45	6.0 ± 2.4	35 ± 22	1.4 ± 1.2
Macoma balthica	SDF	Endo	217 ± 54.8	1.7 ± 0.4	70 ± 42	0.766 ± 0.541	35 ± 13	1.3 ± 1.0	0	0
Mytilus edulis	SF	Epi	0	0	0	0	0	0	7.0 ± 7.0	0.2 ± 0.2
Mollusca, Gastropoda										
Hydrobia ulvae	SDF	Epi	5,261 ± 910.9	6.7 ± 1.2	13,644 ± 1,101	18 ± 2	29,751 ± 6,219	39 ± 7	47,843 ± 5,296	66 ± 7

Table 1 continued

Species	Feed		Mud flat		Zostera meadow		Spartina patch		Spartina marsh	
			Abundance ind m^{-2}	Biomass g AFDW m^{-2}	Abundance ind m^{-2}	Biomass g AFDW m^{-2}	Abundance ind m^{-2}	Biomass g AFDW m^{-2}	Abundance ind m^{-2}	Biomass g AFDW m^{-2}
Littorina littorea	SDF	Epi	0	0	0	0	112 ± 54	2.1 ± 1.5	175 ± 56	3.2 ± 2.0
Nudibranchia	P	Epi	0	0	0	0	49 ± 49	0.107 ± 0.107	0	0
Cnidaria										
Actinaria	SF	Epi	0	0	7.0 ± 7.0	0.003 ± 0.003	274 ± 84	0.777 ± 0.290	168 ± 41	0.54 ± 0.31
Crustacea										
Bathyporeia pilosa	SDF	Endo	7.0 ± 7.0	0.001 ± 0.001	0	0	0	0	0	0
Carcinus maenas	P	Epi	7.0 ± 7.0	0	14 ± 30	0.014 ± 0.010	168 ± 40	1.1 ± 0.5	35 ± 13	0.31 ± 0.15
Corophium arenarium	SDF	Endo	7.0 ± 7.0	0.002 ± 0.002	0	0	0	0	0	0
Crangon crangon	P	Epi	7.0 ± 7.0	0.031 ± 0.031	0	0	0	0	0	0
Gammarus locusta	O	Epi	0	0	0	0	7.0 ± 7.0	0.016 ± 0.016	0	0
Hyale nilssoni	?	Epi	0	0	7.0 ± 7.0	0	0	0	42 ± 23	0.02 ± 0.017
Idotea chelipes	SDF	Epi	21 ± 11.2	0.009 ± 0.008	14 ± 11	0.009 ± 0.007	7.0 ± 7.0	0	0	0
Melita palmata	SDF	Epi	0	0	0	0	14 ± 14	0.003 ± 0.003	0	0
Total			12,964	22.03	22,834	25.27	44,033	59.96	53,160	72.14

Values are average number of individuals per m^{-2} (ind m^{-2} ± SE) and g ash free dry weight per m^2 (g AFDW m^{-2} ± SE), respectively

Functional groups are: *P* predator, *SDF* surface deposit feeder, *SSDF* sub-surface deposit feeder, *SF* suspension feeders, *O* omnivore, *Endo* endofaunal species, *Epi* epifaunal species, *SE* standard error, which was obtained by dividing the SD by the square root of the number of observations

detritus within the sediment (e.g., *Oligochaeta*, *Heteromastus filiformis*); (4) predators (P) that prey on other benthos species (e.g., *Nepthys cirrosa*, *Carcinus maenas*); (5) omnivores (O) that have several feeding strategies (e.g., *Nereis diversicolor*).

Sediment grain size, chl. *a* and organic matter analysis

Sediment samples were analyzed for grain size distribution (median grain size and the mud content being the percentage of silt and clay, i.e., % <63 μm) by laser diffraction technique performed with a Malvern Mastersizer 2000. Particulate organic carbon and nitrogen content of the sediments were analyzed by a Carlo Erba elemental analyzer, type NA-1500. The phosphor content of the sediments was determined by using Perkin Elmer ICP-OES, type Optima 3300DV.

For chlorophyll analysis the freeze dried sediment samples were first homogenized with a mortar. Then approximately 1 g of the sediment was placed with 10 ml 90% acetone in a little pulverize bottle. After the sediment was pulverized, the extract was frozen with liquid CO_2. The extract was then placed in a centrifuge for 3 min at 1,500 rpm. The supernatant was finally placed in the Waters Fluorescentie detector 474 for pigments analysis.

Statistical analysis

Several diversity indices were calculated using PRIMER 5.0 (Clarke 1993), in order to compare benthic assemblages at the different habitats. First, we calculated Margalef's index (d) for species richness, which gives the number of species present for a given number of individuals:

$$d = (S - 1)/\log N$$

where S is the total number of species and N the total number of individuals. Second, species diversity was calculated using Shannon's–Wiener diversity index (H'):

$$H' = -\sum_i p_i \times \log_e(p_i)$$

where p_i is the proportion of the total count arising from the *i*th species. Third, we used Pielou's evenness index (J') to expresses how evenly the individuals are distributed among the different species:

$$J' = H'/H'_{max}$$

where H'_{max} is the maximum possible value of Shannon–Wiener diversity for a given number of individuals and species.

One-way ANOVA with a posteriori Tukey's HSD tests were used to examine between-habitat differences in environmental and faunal properties ($p < 0.05$). Data were tested for normality and heteroscedasticity and, when necessary, square root or log-transformed.

Similarities and differences in macrofaunal assemblages were explored using non-metric multidimensional scaling (n-MDS), based on Bray–Curtis similarity indices on log-transformed, unstandardized data. Stress values indicate how well the solution (two-dimensional MDS plot) reflects the similarities among cores. Values < 0.1 are good and <0.2 are useful (Clarke 1993). Overall and pair-wise comparisons for significant differences in macrofaunal composition between habitats were made using analysis of similarity (ANOSIM) (Clarke 1993). Similarity percentage (SIMPER) analyses were used to determine the percent of similarity of samples and the particular taxa responsible for differences between groups (Clarke 1993). These multivariate analyses (MDS) and the diversity measures were performed with the program Primer 5.0 (Clarke 1993).

Results

Benthic macrofaunal assemblage structure in the four habitats

Multivariate analyses of the benthic macrofaunal assemblages revealed that the macrobenthos distribution over the four habitats (mudflat, *Z. noltii*, *Spartina* patch, *Spartina* marsh) was best separated by species abundance (Fig. 2). Differences were less clear when either taxonomic groups or feeding modes (details in Table 1) were used. Figure 2 shows that the four different habitats are characterized by different assemblages (ANOSIM, $p = 0.001$, $R = 0.73$, in line with hypothesis 2). The mudflat assemblage and *Z. noltii* meadow assemblage showed highest similarities (SIMPER, 69% similarity, ANOSIM, $p < 0.001$, $R = 0.33$), whereas the *Spartina* marsh assemblage showed the highest
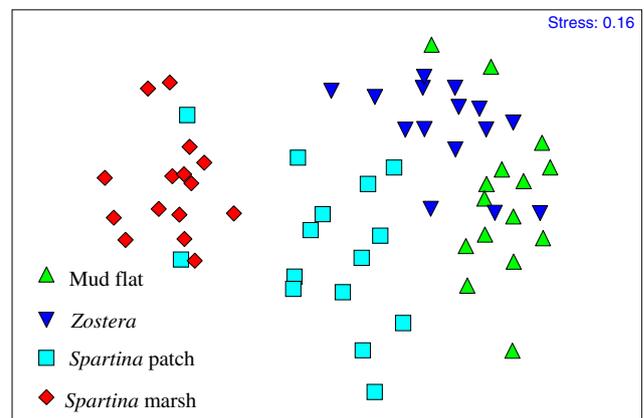
Fig. 2 MDS ordination of species abundance data from the four different areas

dissimilarity with these two areas [SIMPER, 47% (mudflat) and 44% (*Z. noltii*) similarity, ANOSIM, both $p < 0.001$, $R = 0.99$]. The *Spartina* patch assemblage has an intermediate position in the ordination diagram, showing a similarity of 61% with the other habitats (ANOSIM, $p < 0.001$, $R = 0.66$). Below we analyze to which extend these differences in macrobenthic assemblages can be explained by differences in the engineered habitat available to benthos and follow our hypotheses.

Characterization of the (engineered) habitat available to benthos

Both shoot and root biomasses were significantly higher in *S. anglica* than in *Z. noltii*, with highest values in the *Spartina* marsh (Table 2). Shoot density was, however, significantly higher in the *Z. noltii* vegetation. At low tide *Z. noltii* shoots typically lie down on the sediment surface (shoot length on average 15 cm), whereas the stiff *Spartina* stems are typically 30 cm in height. These morphological differences between *Spartina* and *Z. noltii*, cause the different engineering characteristics of both plant species with respect to habitat complexity, reducing hydrodynamic energy, trapping of particulate material and increasing bottom elevation.

Measurements of elevation (meters above NAP, which is similar to mean sea level) revealed that mud flat (1.52 ± 0.01 m NAP) and *Z. noltii* (1.59 ± 0.02 m NAP) areas had roughly the same elevation whereas the *Spartina* vegetation had a slightly, but significantly higher elevation (*Spartina* patch 1.75 ± 0.03 m NAP, *Spartina* marsh 1.69 ± 0.03 m NAP; Table 2). The spatial heterogeneity in elevation is, however, too small to account for major differences in macrobenthic communities. The maximum difference in immersion time between sampling sites was <10% per tidal cycle.

The sediment analysis clearly showed retention of small particles within vegetation (Table 2). Median grain size was significantly higher at mud flat (179 ± 1.8 μm) compared to the vegetated areas (119–138 μm). Mud content (i.e., fraction < 63 μm) was significantly higher in vegetated areas (*Z. noltii* $27 \pm 2.3\%$; *Spartina* patch $18 \pm 2.3\%$; *Spartina* marsh $24 \pm 3.6\%$) than at the unvegetated mudflat ($6.8 \pm 0.64\%$), but no significant differences were observed within the different vegetations (Fig. 3). The particulate organic carbon and organic nitrogen content were highest at the *Spartina* marsh, whereas all other sites had much lower content of a similar magnitude (Fig. 3). A similar pattern was observed for chl. *a* (Fig. 3). Overall it is clear that vegetations have a significant effect on sediment properties, and that differences within the three vegetated habitats were in general small, except for the *Spartina* marsh showing a higher organic material content.

Macrofaunal diversity, abundance and biomass

A total of 38 macrobenthic invertebrate taxa were identified in this study, belonging to six different phyla; 82% were endofaunal species and 18% epifaunal species (Table 1). The mudflat, *Zostera* meadow and *Spartina* patch showed a similar total number of species (24, 22 and 24 species, respectively) and a similar number of endofaunal species (20, 17 and 16), whereas these numbers were much lower in the *Spartina* marsh (13 total, 7 endofaunal; Table 3). The number of epifaunal species was highest in the *Spartina* patch vegetation (8) and lowest at the mud flat (4; Table 3).

Species richness (*d*) was similar for the mud flat (10.2 ± 0.40), *Z. noltii* meadow (9.07 ± 0.55) and *Spartina* patch (9.73 ± 0.55), but significantly dropped in the *Spartina* marsh area (5.73 ± 0.55; Table 3). Endofaunal species richness was highest at the mud flat and was lower in the vegetated areas, especially in the *Spartina* marsh. Epifaunal species richness showed the opposite pattern, with significantly higher values in the *Spartina* patch and

Table 2 Habitat and vegetation characteristics of the four habitats (average $\pm$ SE): elevation (m), shoot dry weight (g AFDW m^{-2}), number of stems (number m^{-2}), roots dry weight (g AFDW m^{-2}), mud content (% <63 μm), median grain size (μm), *Arenicola* sand piles (number m^{-2}) and algae dry weight (g AFDW m^{-2})

	Mud flat	*Zostera* meadow	*Spartina* patch	*Spartina* marsh
Number of stems (number m^{-2})	0	19,683 $\pm$ 1,274[a]	335 $\pm$ 68.3[b]	454 $\pm$ 28.9[b]
Shoot biomass (g AFDW m^{-2})	0	48 $\pm$ 3.5[a]	136 $\pm$ 27.5[b]	338 $\pm$ 30.3[c]
Root biomass (g AFDW m^{-2})	0	185 $\pm$ 24.09[a]	900 $\pm$ 74.9[b]	1,471 $\pm$ 126[c]
Elevation (m NAP)	1.5 $\pm$ 0.01[a]	1.6 $\pm$ 0.02[a]	1.8 $\pm$ 0.03[b]	1.7 $\pm$ 0.03[b]
Mud content (%)	6.8 $\pm$ 0.64[a]	27 $\pm$ 2.3[b]	18 $\pm$ 2.3[b]	24 $\pm$ 3.6[b]
Median grain size (μm)	179 $\pm$ 1.8[a]	119 $\pm$ 6.1[b]	138 $\pm$ 7.6[b]	138 $\pm$ 14.1[b]
Arenicola sand piles (number m^{-2})	63 $\pm$ 2.8[a]	30 $\pm$ 5.1[b]	14 $\pm$ 3.0[c]	0[d]

Elevations are given in meters above the Dutch ordnance level (NAP), which is similar to mean sea level. Letters indicate significant differences among habits using a posteriori Tukey HSD tests

Fig. 3 Average (±SE) mud content, organic matter content (% organic C), nitrogen (% N-Tot.) and chl. *a* content in the four habitats
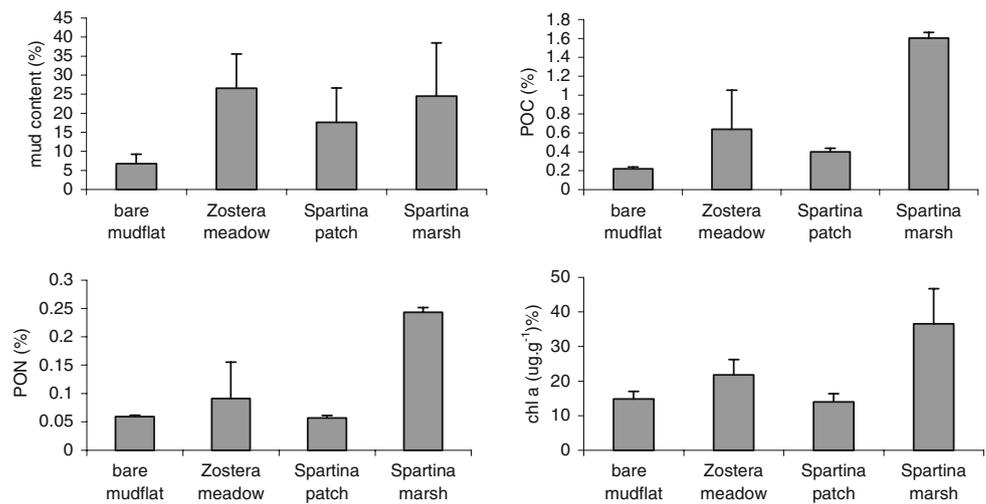
Table 3 Mean (±SE) values for the diversity measures (total number of species, species richness, Shannon–Wiener H' diversity, evenness J'), mean abundance (ind m^{-2}) and mean biomass (g AFDW m^{-2}) observed at each sample site

	Mud flat	*Zostera* meadow	*Spartina* patch	*Spartina* marsh
Total number of species				
Endo	20	17	16	7
Epi	4	5	8	6
Total	24	22	24	13
Species richness (d)				
Endo	8.67 ± 0.39[a]	7.67 ± 0.56[ab]	6.80 ± 0.48[b]	2.67 ± 0.19[c]
Epi	1.4 ± 0.13[a]	1.4 ± 0.13[a]	2.93 ± 0.32[b]	3.07 ± 0.23[b]
Total	10.2 ± 0.40[a]	9.07 ± 0.55[a]	9.73 ± 0.55[a]	5.73 ± 0.55[b]
Shannon–Wiener (H')				
Endo	1.42 ± 0.07[a]	1.38 ± 0.07[a]	0.81 ± 0.08[b]	0.44 ± 0.08[c]
Epi	0.05 ± 0.02[ab]	0.02 ± 0.01[a]	0.19 ± 0.07[b]	0.06 ± 0.01[ab]
Total	1.50 ± 0.04[a]	1.24 ± 0.08[a]	0.93 ± 0.09[b]	0.39 ± 0.04[c]
Evenness (J')				
Endo	0.66 ± 0.03[a]	0.70 ± 0.02[a]	0.43 ± 0.04[b]	0.45 ± 0.08[b]
Epi	0.18 ± 0.05[a]	0.09 ± 0.01[a]	0.16 ± 0.04[a]	0.06 ± 0.01[a]
Total	0.65 ± 0.02[a]	0.57 ± 0.03[a]	0.41 ± 0.03[b]	0.22 ± 0.03[c]
Abundance (ind m^{-2})				
Endo	7,646 ± 1,137[a]	9,148 ± 976[ab]	13,651 ± 1,936[b]	4,890 ± 903[a]
Epi	5,303 ± 914[a]	13,686 ± 1,741[a]	30,382 ± 6,144[b]	48,271 ± 5,330[b]
Total	12,964 ± 1,910[a]	22,834 ± 1,957[a]	44,034 ± 5,878[b]	53,160 ± 5,643[b]
Biomass (g AFDW m^{-2})				
Endo	15 ± 2.3[ab]	7.15 ± 1.41[ac]	17 ± 2.9[ab]	2.09 ± 1.18[c]
Epi	6.77 ± 1.17[a]	18 ± 2.2[b]	43 ± 6.6[c]	70 ± 8.8[d]
Total	22.03 ± 2.71[a]	25.27 ± 2.56[a]	59.96 ± 6.87[b]	72.14 ± 8.67[b]

Endo endofauna, *epi* epifauna

Letters indicate significant differences among habits using a posteriori Tukey HSD tests

Spartina marsh as compared to the *Zostera* meadow and the bare mud flat (Table 3). Total and endofaunal diversity (H') and evenness (J') was similar at the mud flat and *Zostera* meadow, but significantly lower in the *Spartina* patch and *Spartina* marsh. Epifaunal diversity and evenness showed low values without a clear pattern (Table 3).

Total mean abundance (individuals m^{-2}) and biomass (g AFDW m^{-2}) followed the sequence bare mudflat < *Zostera* meadow < *Spartina* patch < *Spartina* marsh (Table 3). This increase was mainly due to the increase in epifaunal abundance and biomass in the vegetated areas. It is noted that the increase in epifaunal

abundance was mainly due to a huge increase of a single species: the gastropod *H. ulvae* (Table 1). Endofaunal abundance showed a different pattern, with the highest abundances in the *Spartina* patch, followed by the *Zostera* meadow, the mud flat and the lowest abundance in the *Spartina* marsh. This pattern was not reflected in the biomass, indicating that individuals in the *Spartina* patch vegetation were on average much smaller than on the mudflat. Endofaunal abundance and biomass were lowest in the *Spartina* marsh (Table 3).

Macrofaunal functional groups as defined by feeding modes

As the interaction of ecosystem engineering vegetations with hydrodynamic conditions may affect supply of food to specific macrobenthic feeding modes, we classified all animals in five functional groups. Table 4 summarizes the results for the macro-benthic species that contribute quantitatively most to each feeding mode. This table suggests that the division in endo- and epibenthos is more important for explaining the distribution of animals over habitats, than feeding types. The *Spartina* data reveal that patch size is also highly important.

The abundance (Fig. 4) and biomass (Fig. 5) of SDFs that typically feed on diatoms on the surface of the sediment were dominated by the epibenthic gastropod grazer *H. ulvae*. It is clearly seen that both the abundance and the biomass increases in the following order: bare mudflat < *Zostera* meadow < *Spartina* patch < *Spartina* marsh. Compared to this effect, changes in endobenthic SDFs are small (Fig. 4, 5), but showing the opposite trend as for the epibenthic SDF. That is, endobenthic SDF are nearly absent in the *Spartina* habitats, and show highest densities in the *Zostera* meadows and the bare mudflat.

The abundance of SSDF that predominantly feed on micro-organisms, phytobenthos and detritus was highest in the small *Spartina* patches, and equal in all other habitats (Fig. 4), although contributing species clearly differ between habitats (Table 1). Combining the biomass data (Fig. 5) with the abundance data (Fig. 4), indicates that only small animals can live in the *Spartina* marsh and small *Spartina* patches.

Suspension feeders were not very abundant at the study site, due to the high tidal level of the sampling stations. They appeared to be most abundant in the small *Spartina* patches, where epi- and endobenthic SFs could co-exist (Fig. 4). In the *Zostera* meadow and at the mudflat, the abundance of epibenthic SFs was negligible. In the *Spartina* marsh, the abundance of the endobenthic SFs diminished, whereas there was still an epibenthic assemblage of SFs present (Fig. 4). The biomass of the

Table 4 Overview indicating for the most important macro-benthic species, how the species abundance in three vegetated sites (*Zostera* meadow, *Spartina* patch and *Spartina* marsh) compare to that at the mud flat

Functional groups	Species		Mud flat → *Zostera* meadow	Mud flat → *Spartina* patch	Mud flat → *Spartina* marsh
Sub-surface deposit feeders	*Arenicola marina*	Endo	(−)	−	×
	Capitella capitata	Endo	−−	(−)	×
	Heteromastus filiformis	Endo	(+)	(+)	−−−
	OLIGOCHAETA	Endo	(−)	++	(+)
Surface deposit feeders	*Malacoceros*	Endo	(+)	(-)	×
	Tharyx marioni	Endo	(+)	(-)	×
	Macoma balthica	Endo	−−−	−−	×
	Pygospio elegans	Endo	(+)	−−−	×
	Streblospio shrubsolii	Endo	(−)	(−)	×
	Hydrobia ulvae	Epi	+++	+++	+++
	Littorina littorea	Epi	×	+	+++
Suspension feeders	*Polydora ligni*	Endo	++	×	×
	Cerastoderma edule	Endo	(−)	(+)	−
	Actinaria	Epi	(+)	+++	+++
Omnivores	*Nereis diversicolor*	Endo	(−)	(+)	(+)
Predators	**Carcinus maenas**	Epi	(+)	++	(+)
	Nemertea	Endo	(+)	++	(+)

The symbols used in the table have the following meaning: (+) or (−) indicates an increasing or decreasing trend, but no significant differences ($p > 0.05$, One-way ANOVA); + or − indicates an increase or decrease with $p < 0.05$; ++ or −− the same for $0.05 < p > 0.01$; +++ or −−− the same for $p < 0.001$; × indicates that the abundance was reduced to 0
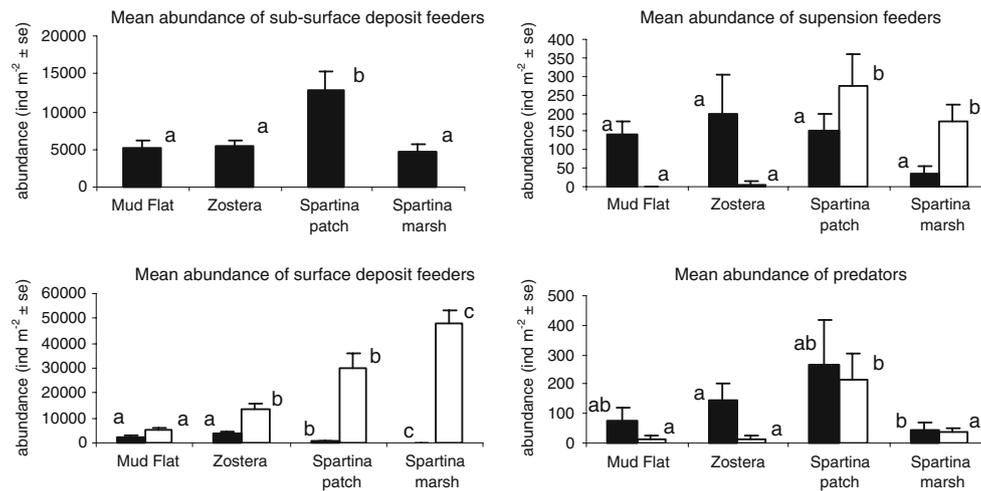
Fig. 4 Mean abundance (ind m^{-2} ± SE) observed for each feeding mode at the four different habitats. *Closed bars* represent endofauna, *open bars* epifauna. Endofaunal and epifaunal averages were analyzed separately for significant differences between the four habitats. *Letters* indicate significant differences among habits using a posteriori Tukey HSD tests

epibenthic SFs was in all cases low compared to that of the endobenthic SFs (Fig. 5).

The predators (P) that prey upon other benthos species showed a comparable pattern as that of the SFs, in that they were most abundant in the small *Spartina* patches, where both epi- and endobenthic predators could co-exist (Fig. 4). The epibenthic predator *Carcinus maenas* was most abundant (Fig. 4) and had highest biomass (Fig. 5) in the small *Spartina* patches. In all other habitats their abundance was negligible, but they did have a significant biomass in the *Spartina* marsh. The endobenthic predators (*Nemertea*) appeared to be most abundant at the *Spartina* patches, and least abundant at the *Spartina* marsh, although not significant.

Discussion

Several studies demonstrated opposite effects of ecosystem engineers on species richness and abundances (Jones et al. 1997; Crooks 2002; Wright and Jones 2004), complicating the identification of underlying mechanisms. We test a number of hypothesis related to the importance of habitat complexity, productivity and scale for effects of ecosystem engineers on biodiversity, using intertidal flats as a model system. We observed that macrobenthic assemblages significantly differ when comparing two co-occurring vegetations with contrasting ecosystem engineering strength (*Z. noltii* and *S. anglica*; cf. Bouma et al. 2005) and the nearby non-engineered mudflat. The sometimes
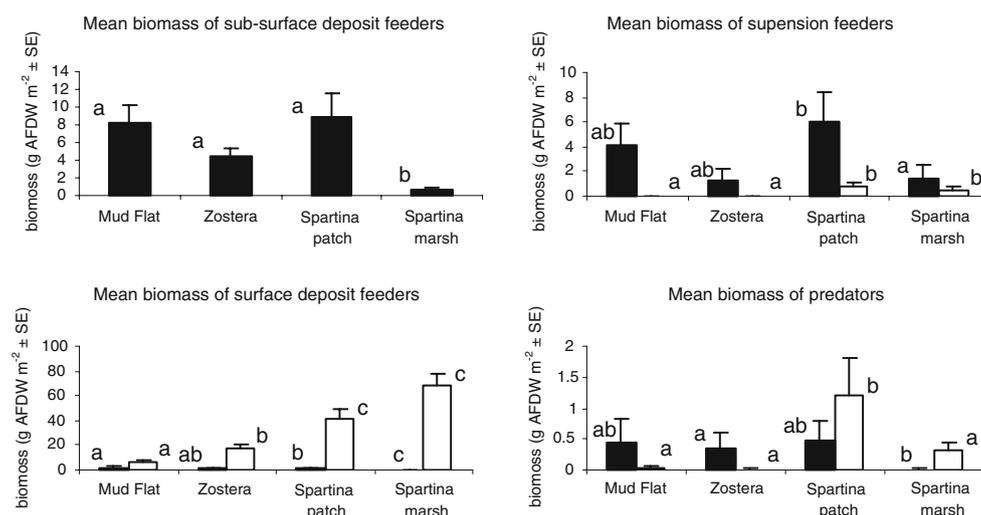
Fig. 5 Mean biomass (g AFDW m^{-2} ± SE) observed for each feeding group at the four different areas. *Closed bars* endofauna, *open bars* epifauna. Endofaunal and epifaunal biomasses were analyzed separately for significant differences between the four habitats. *Letters* indicate significant differences among habits using a posteriori Tukey HSD tests

relatively high values for similarity between the four different habitats, reflect that many differences are mainly expressed as major shifts in dominance of co-occurring species, rather than a complete shift in species composition. Our results most strongly supported hypothesis 3, stating that the increased above-ground habitat complexity in the presence of vegetations support a shift from endo- towards epibenthic species. This shift appears to be much more important than changes in feeding type, refuting our hypothesis 2. In line with hypothesis 4, we found a more diverse benthic macrofaunal assemblage in small *Spartina* patches than in larger *Spartina* meadows. In line with hypothesis 1, we also observed more fine-grained sediment in the vegetated habitats, relative to the unvegetated tidal flat. *Spartina* habitats were also more elevated compared to the unvegetated mudflat and the *Zostera* meadow. This agrees well with several studies describing increased sediment deposition rates and reduced particles sizes in vegetated habitats relative to unvegetated tidal flats, due to the attenuation of tidal and wave energy by the plants (e.g., see Fonseca and Cahalan 1992; Yang 1998; Leonard et al. 2002; Neira et al. 2006). Abiotic differences within the three vegetated habitats remained, however, small: sediment grain size was similar; only POC and chl. *a* showed an increased concentration in the *Spartina* marsh. These observations suggest that sediment properties and soil chemistry, which have been shown to be a major factor in other areas (e.g., Neira et al. 2006), are not primarily driving the faunal differences in our system. Overall, our results suggest that increased above-ground habitat complexity by vegetations supports a shift from endo- towards epibenthic species (cf. hypothesis 3), and that this effect is affected by patch size (cf. hypothesis 4) and not as much by a change in sediment properties (refuting hypothesis 1) or feeding type (refuting hypothesis 2).

The epibenthos in the vegetated areas was strongly dominated by the small diatom-grazing snail *H. ulvae*, which was especially clear for *Spartina*, and in accordance with previous observations (for seagrasses, see Bostrom and Bonsdorff 1997; Bachelet et al. 2000; Blanchet et al. 2004; Cottet et al. 2007; for salt marsh plants see Kneib 1984; Mc Corry and Otte 2000; Whaley and Minello 2002; Cottet et al. 2007). It is not clear to which extend this increase is due to enhanced food availability (cf. suggestion Blanchet et al. 2004) rather than ecosystem engineering. According to previous studies, this opportunistic small gastropod may respond to the high organic matter content (Bostrom and Bonsdorff 1997) and the food present on the macrophytes blades (cf. found for *Bittium reticulatum*; Curras et al. 1993). However, we expect this shift for an important part to be caused by a combined effect of protection against predation and sheltering from hydrodynamic forces by the enhanced habitat complexity. Unfortunately, the descriptive nature of our study does not provide in depth insight in the underlying processes.

Overall, our results agree with the general finding that engineering species that increase habitat complexity also tend to increase the diversity and/or the abundance of organisms (Crooks 2002). Our results show a clear increase in abundance in the vegetated areas, but this is because one or a few species became very abundant (increased dominance), rather than by an increased species diversity. The effect of structural complexity of macrophyte vegetations like seagrasses and salt marsh species, have been well described with respect to protection from predation, reduction of current velocity, retention of particle and the accretion of sediment. Several studies show that these physical changes tend to increase macrofaunal species richness and/or abundances (seagrasses: Orth 1992; Heck et al. 1995; Bartholomew, 2002; salt marsh plant: Rader 1984; Netto et al. 1997, Netto and Lana 1999; Whaley and Minello 2002; Brusati and Grosholz 2006), but with exceptions, especially for the salt marsh species (e.g., Moseman et al. 2004; Neira et al. 2005; Levin and Talley 2000). The contrasting influence of *Spartina* species on macrobenthos composition may be due to conditional outcomes of ecosystem engineering. For other systems, it has been demonstrated that depending on the physical forcing, effects of ecosystem engineers on biodiversity may be quite different (Norkko et al. 2006). Another explanation for variable outcomes of increased structural complexity might be that in some systems, predators themselves may also benefit from protection against predation, thereby increasing predation rates on other smallest infaunal species (Bowden et al. 2001). According to Cottet et al. (2007), other stresses may limit the structuring effect of increased habitat complexity on infaunal assemblages. In case of *Zostera*, *Spartina* and bare mudflat located at high elevations, desiccation may become the dominant stress factor determining infauna community structure. This would partly fit present results, but does not explain the observation that the increased above-ground habitat complexity in the presence of vegetations support a shift from endo- towards epibenthic species (cf. hypothesis 3). Effects of the habitat complexity on recruitment of larvae and the re-suspension of adults (Neira et al. 2006) as well as other factors such as food availability might also play a role.

It is well recognized that ecosystem engineering effects on macrofaunal distributions are hard to separate in effects via food availability versus effects via physical habitat modification, including habitat complexity (Heck and Orth 1980; Irlandi and Peterson 1991; Jones et al. 1994). For example, whereas it was originally thought that the distributions of three species of the fiddler crab *Uca*, were due to food availability, Ringold (1979) demonstrated that this

was due to the root mat density of *Spartina*. Amphipod population growth has been shown to be a complex mixture of refuge against predation and food between seagrasses and macroalgae habitats (Corona et al. 2000). However, in vegetated areas, blue crab growth has been demonstrated to be predominantly controlled by food availability rather than protection from predation (Seitz et al. 2005). Shading effects of the vegetation can play an important role in determining the main food source to benthic assemblages (Whitcraft and Levin 2007). Levin et al. (2006) observed a trophic shift in sediments invaded by *Spartina* compared to uninvaded sediments, with a shift from an algae-based to a detritus-based food web. If we consider only the endo-benthic part, SSDFs (*Heteromastus*, oligochaetes) become indeed relatively more important in the *Spartina* habitats as compared to the *Zostera* meadow and the bare mudflat. However, when including the epibenthic part, a different picture emerges, with an increased importance of SDFs and grazers. This again stresses the importance of including epibenthic fauna when studying salt marsh ecosystem engineers. In line with previous studies that underline the difficulty in assessing most important factors in explaining macrobenthic distributions in- and outside engineered areas, we also cannot provide general statements on the relative importance of food availability versus physical habitat modification. In our particular case, food availability seems to be of lesser importance than habitat modification and habitat complexity. More important, the present study suggests how comparison of ecosystem engineers with contrasting extend on habitat modification, adds strength to the analysis.

A complicating factor when comparing *Z. noltii* and *S. anglica*, is that in addition to above-ground differences, species also differ below-ground. The much higher root mass and sediment compaction in *Spartina* sites may physically hamper establishment and survival of endo-benthic species (e.g., Brusati and Grosholz 2006). For example, sediment compaction and fine grain size distribution hampers settlement of *A. marina* in *Spartina* patches (van Wesenbeeck et al. 2007). Although we observed *Arenicola* in both the *Zostera* meadow and the small *Spartina* patches, this species was completely absent in the *Spartina* marsh. Earlier studies also suggested that polychaetes abundance is negatively influenced by the presence of vegetation since the root/rhizome system of macrophytes hamper these worms to penetrate into the sediment and sustain burrows or tubes (Stoner 1980; Orth et al. 1984; Webster et al. 1998; Hily and Bouteille 1999; Brusati and Grosholz 2006). Since the root/rhizome system in *Zostera* is less dense than that of *Spartina* and sediment is less compacted in *Zostera* meadows, small endobentic species may be able to penetrate the sediment in the presence of seagrasses (Brenchley 1982, this study). The only two

annelid species that were abundantly present in the *Spartina* vegetation were the polychaete *Heteromastus filiformis* and oligochaetes. Both are small, sub-surface deposit feeding species, often reported in other studies to be common in *Spartina* vegetations (e.g., Neira et al. 2005, 2007). Particularly oligochaetes can reach high abundances in salt marshes, as they can live in the microhabitat created by the root system of the plants and are capable to feed upon *Spartina* detritus (Levin et al. 2006).

The root/rhizome of both *Z. noltii* and *S. anglica* seemed to affect bivalve's abundances. The clam *M. balthica* was more harmed where vegetation was present probably because it burrows deeper than the cockle *Cerastoderma* and the vegetation's root/rhizome system preclude *M. balthica* to penetrate into the sediment. Cockles observed at *Spartina* marsh were bigger than the cockles from the unvegetated area (i.e., 0.4 vs. 0.3 g, respectively, cf. Table 1) suggesting that cockles able to settle in the vegetation can reach bigger sizes likely due to a reduction of predation by birds similar to shown for comparable systems (Irlandi and Peterson 1991; Irlandi 1994). Cockles in the *Spartina* habitats typically were living almost on top of the sediment, whereas on the mudflat cockles lived typically a few cm burrowed into the sediment.

In addition to the generalized idea that macrophytes structural density enhances macrofaunal densities (Heck and Orth 1980), a patchy distribution and the presence of edges have been found to support higher faunal densities than continuous or dense patches. For example, patchy/fragmented seagrass systems were found to support higher densities of blue crab juveniles (Hovel and Lipicius 2001), macrofauna (Bowden et al. 2001) and epifauna (Healey and Hovel 2004), although other factors like predation and foraging rates can be higher in patchy areas (Irlandi and Peterson 1991; Irlandi 1994, 1996; Irlandi et al. 1995). Present results underlined the importance of patchiness in structuring macrofaunal assemblages as well, as we found significantly higher species richness at the *Spartina* patch than *Spartina* marsh. A more diverse assemblage was observed in the *Spartina* patch, as both endo- and epibenthic species were present. The *Spartina* patch area allowed more species to be present and enhanced the abundances of some of them. Together with patchiness, also the time the ecosystem engineer being present may be important. Assuming that smaller *Spartina* patches have been established more recently, the sediment of the *Spartina* patches have a significantly lower below-ground biomass, indicating a less densely rooted and compacted sediment as compared to the *Spartina* marsh which is already present for several years. This allowed a significantly higher endofaunal species richness, abundance and biomass in the *Spartina* patch as compared to the *Spartina* marsh. Along a sequence of stages in the invasion of a hybrid *Spartina*,

from tidal flat to dieback, Neira et al. (2007) observed cascading changes in sediment conditions that led to a substantial reduction in macrobenthic species richness, increased dominance and a shift in feeding modes.

Summarizing, our approach comparing two ecosystem engineering species of different strength, revealed large differences in biodiversity effects when compared to the bare mudflat. Conclusions about the mechanisms underlying these effects are hampered by the fact that these two species differ in many aspects. The use of artificial structures that mimic a single ecosystem engineering aspect would therefore be a useful tool for comparing natural species. Nevertheless, present results clearly show that (1) epibenthic vegetations of *Z. noltii* and *Spatina anglica* cause a shift in macrofaunal assemblages from endo- towards epibenthic macrobenthic species (cf. hypothesis 3) and that (2) there were no clear patterns related to feeding modes (refuting hypothesis 2) and sediment properties (refuting hypothesis 1). This suggests that increased above-ground habitat complexity is probably the main mechanism driving macrobenthic biodiversity in our system, and that food availability/productivity was of lesser importance. In addition, enhanced patchiness also has a distinct positive effect on biodiversity (cf. hypothesis 4). Finally, the distinction between epibenthic and endobenthic macrofauna turned out to be very important to better understand faunal differences between engineered and non-engineered habitats.

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