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Facilitative effects of introduced Pacific oysters on native macroalgae are limited by a secondary invader, the seaweed *Sargassum muticum*

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ABSTRACT

Introduced habitat-providing organisms such as epibenthic bivalves may facilitate the invasion and expansion of further non-native species which may modify the effects of the primary invader on the native system. In the sedimentary intertidal Wadden Sea (south-eastern North Sea) introduced Pacific oysters (*Crassostrea gigas*) have overgrown native blue mussel beds (*Mytilus edulis*). These oyster beds are now providing the major attachment substratum for macroalgae. Recently, oysters have expanded their distribution into the shallow subtidal zone of the Wadden Sea, and there support a rich associated species community including the Japanese seaweed *Sargassum muticum*, which has been presumably introduced together with the oysters. With a block designed field experiment, we explored the effects of *S. muticum* on the associated community of soft-bottom *C. gigas* beds in the shallow subtidal. Replicated oyster plots of 1 m^2 were arranged with a density of 0, 7, 15 or 45 *S. muticum* m^{-2}, respectively. We found no effects of different *S. muticum* densities on associated epi- and endobenthic community compositions associated to the oyster plots. However, the overall coverage of sessile organisms settling on the oyster shells was significantly reduced at high *S. muticum* densities. The occurrence of abundant native macro-algal species such as *Polysiphonia nigrescens*, *Antithamnion plumula* and *Elachista fucicola* decreased with increasing *S. muticum* densities. Sessile invertebrates, by contrast, were only marginally affected and we found no effects of *S. muticum* canopy on diversity and abundance of endofauna organisms. We conclude that increasing densities of *S. muticum* on *C. gigas* beds in the shallow subtidal zone of the Wadden Sea limit the occurrence of native macroalgae which otherwise would benefit from the additional hard substratum provided by the oysters. Thus, a secondary invader may abolish the effects of the primary invader for native species by occupying the new formed niche.

1. Introduction

Introduced marine species can cause major effects on the recipient community by changing physical factors, community structure and ecosystem properties (e.g. Callaway and Josselyn, 1992; Bruno, 2000; Grosholz et al., 2000; Crooks and Khim, 2002; Ruesink et al., 2006). Jones et al. (1994) established the term ecosystem engineer for “species that modulate the availability of resources, by causing major changes in biotic and abiotic materials”. Coastal environments may be strongly affected if invasive species are ecosystem engineers that provide new habitats in recipient systems (Crooks and Khim, 2002; Cuddington and Hastings, 2004; Buschbaum et al., 2006; Wallentinus and Nyberg, 2007; Sousa et al., 2009). The additional structures may facilitate the invasion of further non-native species. This positive interaction of non-indigenous species is termed ‘invasional meltdown’ and may cause accelerated effects on recipient ecosystems (Simberloff and Von Holle, 1999).

In addition to molluscs, macroalgae are regarded as important habitat-providing invasive marine engineers (Reise et al., 2002; Gutiérrez et al., 2003; Schaffelke et al., 2006; Borthagaray and Carranza, 2007; Schaffelke and Hewitt, 2007; Wallentinus and Nyberg, 2007; Buschbaum et al., 2009; Sousa et al., 2009). Non-native algae may alter the recipient community by increasing structural complexity that may enhance species richness and diversity (Crooks and Khim, 2002; Buschbaum et al., 2006). They may also affect algal and faunal understorey assemblages by modifying physical factors such as water flow (Velimirov and Griffiths, 1979; Eckman et al., 1989; Duggins et al., 1990; Russell, 2007), sedimentation rate (Eckman et al., 1989; Connell, 2005) and light conditions (Kennelly, 1989; Connell, 2003; Toohey et al., 2004; Connell, 2005). In addition, sweeping algal fronds can affect other sessile organisms such as barnacles by scouring the substratum (Leonard, 1999; Irving and Connell, 2006).

A very successful invasive alga is the Japanese seaweed *Sargassum muticum* (Yendo) Fensholt (Phaeophyceae, Fucales) which was first

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described from Japan and has currently an almost worldwide distribution (Critchley et al., 1990b). In the European Wadden Sea, it was first detected in the western part near the island of Texel in 1981 and reached the northern Wadden Sea in 1994 (Schories and Albrecht, 1996; Wolff, 2005). Reasons for its very efficient spreading are the physiological traits of the germlings (Hales and Fletcher, 1989) and its high reproductive potential (Fletcher, 1980; Norton, 1981). Germlings of *S. muticum* are tolerant to a wide range of salinities, temperatures and light regimes (Hales and Fletcher, 1989). The alga is self-fertilizing and its fronds are breaking off in late summer serving as floating vehicles for propagules (Fletcher, 1975, 1980; Norton, 1977, 1981). An additional dispersal vector is human mediated transport with the Pacific oyster *Crassostrea gigas* (Thunberg) (Druehl, 1973; Critchley and Dijkema, 1984). The occurrence of *S. muticum* in an invaded area depends on the availability of hard substratum and is restricted by physical factors such as strong wave action, high sedimentation rates and limited light conditions (Viejo et al., 1995; Thomsen, 2006).

S. muticum has usually been considered an ecosystem engineer because it may influence a number of physical factors such as light conditions beneath dense seaweed canopies and might also affect water flow, sedimentation rate, water temperature and nutrient composition within algal beds (Critchley et al., 1990a,b; Britton-Simmons, 2004; Strong et al., 2006; Domisch, 2008). These changes in abiotic conditions may cause different effects on recipient algal assemblages (Olabarria et al., 2009; Sánchez and Fernández, 2005). Negative effects of *S. muticum* on diversity and abundance of native algal communities are reported from western Pacific coasts (from British Columbia through Washington State to California) and also from European coasts (Denmark, Scotland and Spain) (Ambrose and Nelson, 1982; de Wreede, 1983; Viejo, 1997; Staehr et al., 2000; Britton-Simmons, 2004; Harries et al., 2007). However, also facilitating effects on species numbers and diversity of less dominant algae of an invaded assemblage were observed. For example, at the north coast of Spain (north-east Atlantic) Sánchez et al. (2005) found that abundance of dominant native species may be reduced but total resident algal species number and diversity increased after establishment of *S. muticum*. Similar to consequences of *S. muticum* introduction on native algae the effects on resident benthic invertebrates may also be variable. On the Pacific coast of North America, for instance, invertebrate communities were not affected by *S. muticum* (Britton-Simmons, 2004) while at coasts of the Irish Sea and the English Channel (north-east Atlantic) soft-bottom assemblages were different inside and outside *S. muticum* canopies (Strong et al., 2006). Consequently, effects of *S. muticum* introduction may be different and strongly depend on the considered variables in the native system (Williams and Smith, 2007).

In the sedimentary environment of the Wadden Sea, Buschbaum et al. (2006) revealed that *S. muticum* increases associated epibiota diversity because *S. muticum* provides a habitat which is much more structured than native macroalgae occurring in the area. However, for the area no studies exist that investigate the impacts of *S. muticum* on the habitat it is attached to. Shortly after its introduction, *S. muticum* predominantly used epibenthic mussel beds of *Mytilus edulis* L. for recruitment which represented the major hard substratum available. However, within the last 5 years a dominance shift from native mussels to Pacific oysters *C. gigas* occurred and oyster shells are representing today the dominant attachment substratum for *S. muticum* (Polte and Buschbaum, 2008). The rapid shift from mussel beds to aggregations dominated by oysters caused changes in the associated species assemblage (Diederich et al., 2005; Kochmann et al., 2008; Reise, 2008). In the shallow subtidal zone, this habitat is currently changing again because oyster beds become increasingly overgrown by *S. muticum*. Therefore, this study focuses on the impacts of *S. muticum* overgrowth on the associated species community of an oyster bed and investigates the scenario that *S. muticum* abundances will further increase in the future. We hypothesized that *S. muticum* coverage affects species abundance and diversity of an oyster bed and that these effects depend on *S. muticum* density. To explore these hypotheses we performed a field experiment with different *S. muticum* densities on experimental oyster plots. The aim was to answer the following questions: (i) Does a *S. muticum* canopy affect the endobenthic community of an oyster bed? (ii) Does a *S. muticum* canopy have an impact on the recruitment of sessile faunal and algal species settling on oyster shells? (iii) Do the effects depend on *S. muticum* density?

2. Materials and methods

2.1. Study site

Investigations and experiments were performed in a sheltered bay named "Königshafen" at the island of Sylt (54°55′N, 008°20′E) in the northern Wadden Sea (German Bight, North Sea) (Fig. 1). The bay is drained and flooded by a tidal creek. The semi-diurnal tides in this area range up to 2 m. Mean water temperatures vary from 15 °C in summer to 4 °C in winter. Average salinity is 30 and maximum near-bottom current velocities range between 0.3 and 0.5 m s^{-1} (Austen, 1994a). Detailed descriptions of geology, hydrodynamics and sediment composition in the area can be found in Bayerl and Higelke (1994) and Austen (1994a,b). Further information on biota is given by Reise (1985), Reise et al. (1989, 1994) and Schories et al. (1997).

2.2. Experimental design

A field experiment was established to test the influence of *S. muticum* canopies on oyster bed communities in the shallow subtidal zone (0.3–0.5 m below mean low water tide level) of the Wadden Sea. The experiment was set up on a sand flat in close proximity to an oyster bed where *S. muticum* naturally occurs (Fig. 1). Each experimental unit (plot) had a size of 1 m^2 and consisted of 160 individuals of *C. gigas* collected from the oyster bed nearby (Fig. 2a). The oysters were carefully transplanted together with the associated species assemblage to ensure a natural community at the beginning of the experiment. Previous studies revealed that *S. muticum* density in the study area is about 7–10 individuals m^{-2} and remains stable from the end of April to October (Buschbaum et al., 2006; Polte and Buschbaum, 2008). Experimental plots with four *S. muticum* density treatments were established: (i) no *S. muticum*, (ii) density of 7 individuals m^{-2}, (iii) density of 15 individuals m^{-2} and (iv) a density of 45 individuals m^{-2}. Densities were kept constant during the experimental period (end of April to October 2007) by adding algal thalli when they were lost. We used density treatments instead of coverage since cover is changing with ongoing seasonal growth of the *S. muticum* thalli. The four density treatments were arranged in a randomized block design with 4 blocks each comprising 5 experimental units. Each block contained every density treatment ensuring full orthogonality of the experiment which enabled us to test for block effects (Fig. 2c). Additionally, each density treatment was replicated in one of the blocks to test for possible interactions between treatment and block factor.

2.3. Sampling

2.3.1. Sessile organisms

To test for effects of *S. muticum* on the recruitment of sessile species living attached to an oyster bed we chose oysters with a shell length of 150 to 160 mm from which we carefully removed all epibionts and used them as a recruitment matrix. Experiment beginning was two weeks after establishment of the plot at the end of April 2007. For each plot 20 cleaned oysters were marked and randomly placed in the inner part (>20 cm from edge). After an

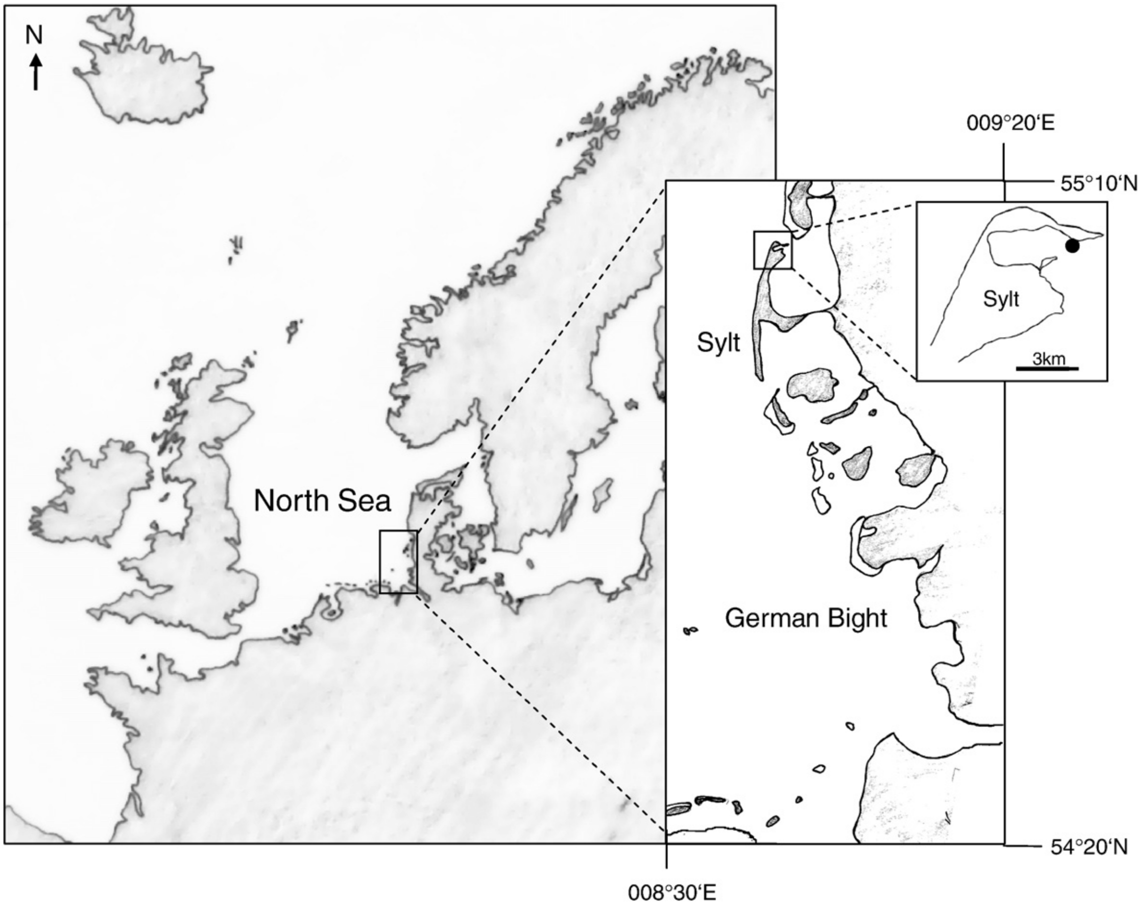

Fig. 1. Study site (●) at the northern tip of the island of Sylt (German Bight, North Sea).

experimental period of 3 months (July 2007) and 6 months (October 2007), 10 marked oysters per plot were randomly sampled, respectively. Oysters were taken to the laboratory and sediment was carefully removed by rinsing them over a sieve. Afterwards, sessile macroscopic algae and invertebrates were identified to species (or nearest possible taxonomic) level using a stereomicroscope.

For each oyster, percentage cover of all attached species was determined to the nearest 5%. Individual numbers of sessile faunal species (e.g. barnacles) were additionally counted and their abundance oyster^{-1} determined. This was not done for macroalgae due to difficulties in distinguishing single individuals in most species.

2.3.2. Endobenthic organisms

The infauna was sampled once in August 2007 during low tide. Samples were taken by using a tube corer of 5 cm of diameter (sampling depth: 5 cm). To compensate for a possible patchy distribution of organisms, six samples were randomly taken from the inner part of each plot (>20 cm from edge, Fig. 2b) and pooled afterwards (total sample volume 98 cm^3). Samples were washed over a sieve of 250 µm mesh size and organisms retained were counted and determined to species (or nearest possible taxonomic) level using a stereomicroscope.

2.4. Water flow measurement

The relative near-bottom water velocity within the experimental plots was measured by means of weight loss of gypsum pieces. Gypsum (Bob Stone® DIN1168) was filled into muffin forms embedding plastic sticks for later fixation. The muffins were dried for one week at 50 °C, fixed with the plastic sticks to iron rods using cable ties and then placed in the inner part of the experimental plots from September 28 to September 29, 2007. One gypsum muffin per plot was positioned 10 cm above the bottom and thus right above the oysters. After 24 h (spanning two high tides and one low tide) muffins were brought to the laboratory and weighted after being dried again (at 50 °C for 7 d). Weight loss was determined and used as a proxy of flow velocity in the treatments (method similar to Eckman et al., 1989).

2.5. Sediment characteristics

To test for effects of *S. muticum* overgrowth on sedimentation within an oyster reef we determined sedimentation rate within the experimental plots. Bottles with a volume of 500 ml, an opening diameter of 3.5 cm and a height of 21 cm were used as sediment traps. The ratio of height to width of the used bottles was 6:1 and within the range recommended by Gardner (1980) for water velocities higher than 0.15 m s^{-1}. Flow velocity at our study area ranges from 0.3 to 0.5 m s^{-1} (Austen, 1994a). For better handling each bottle was put in a PVC tube with a diameter of 10 cm which was placed randomly in the inner part of each plot. The opening of the tube was on the same height as the top of the oysters preventing oyster faeces from falling into the bottles. Additionally, the tube opening was covered with a net (mesh size of 6 mm) to prevent mobile organisms such as crabs from entering into the trap. Sediment was collected for 14 d from August 23 to September 5, 2007 spanning a neap-spring tidal period using one

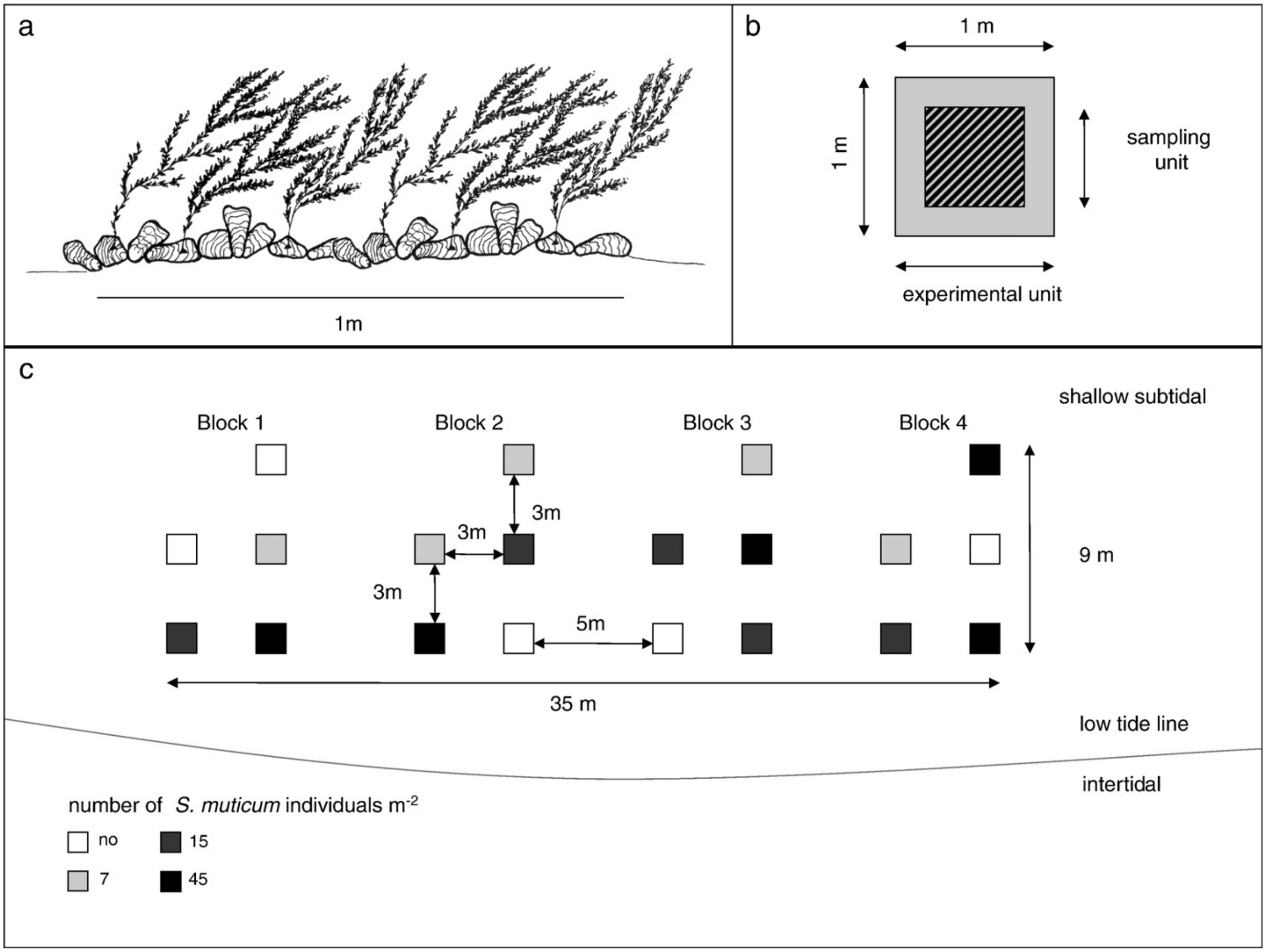

Fig. 2. Experimental set-up. (a) Schematic drawing of an experimental plot with *Crassostrea gigas* covered by *Sargassum muticum*. (b) Experimental unit. Samples were only taken from the inner part to avoid edge effects. (c) Arrangement of the experimental plots in four blocks.

sediment trap per plot. At the end of the experiment, trapped sediment was washed with freshwater to remove salt and dried afterwards. To analyse sediment grain size distribution the dry sediments were shaken in a stack of five sieves with decreasing mesh sizes (mesh sizes: 1000, 600, 250, 125, and 63 µm) for 6 min and fractions were weighted to the nearest 0.1 g.

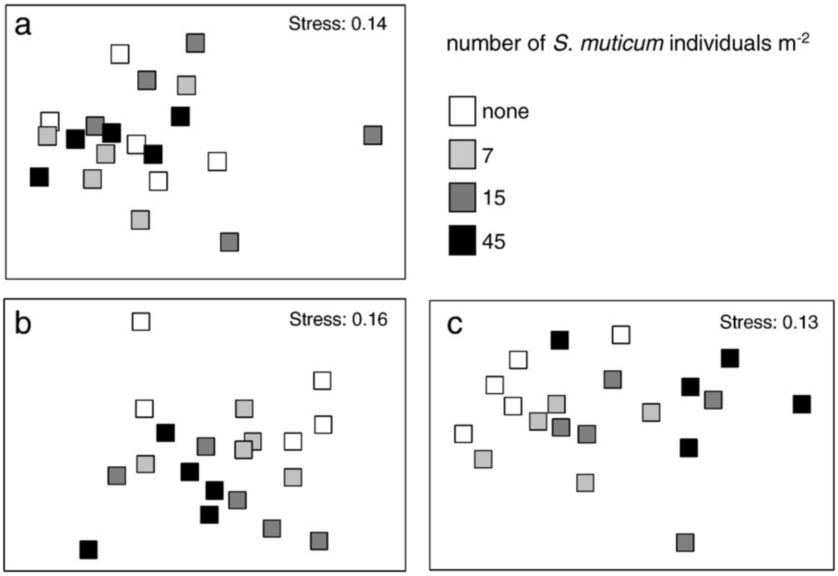

Fig. 3. MDS plots of species assemblages based upon Bray–Curtis similarities. (a) Endobenthic organisms (b) epibenthic organisms — July and (c) epibenthic organisms — October.

2.6. Statistical analysis

Analysis of variance (ANOVA) was used to test for differences in species abundances (epibionts and endofauna) and abiotic factors (flow velocity and sedimentation rate). The randomized block design was used to test for spatial heterogeneity between block sites. *S. muticum* density was used as a fixed factor and the block as random factor. Interactions between block factor and treatments showed no significance ($p > 0.05$). Only in one case (effects of *S. muticum* occurrence on the abundance of *B. crenatus* in July) a significant effect was found ($p = 0.048$) and we decided to neglect interactions to enhance the power of the analysis (Underwood, 1997). All data were tested for homoscedasticity using Cochran's test. Abundance data needed to be log $(x+1)$ transformed to fulfill homogeneity of variances. The post-hoc Tukey HSD test was used for comparisons between different *S. muticum* densities.

Community analysis was conducted using multivariate, non-parametric ordination technique (Multidimensional Scaling) based upon the Bray–Curtis similarity comparisons with the Primer TM software (Clarke and Warwick, 2001). For analyses of similarity (ANOSIM) of epibenthic communities we worked with percent coverage oyster^{-1} data while we used abundance data for the analyses of endobenthic communities.

Results are presented as means with standard deviation. Effects were considered to be statistically significant if p-value was <0.05.

3. Results

3.1. Community responses

We detected no differences in the community composition between treatments with different *S. muticum* density neither in the endobenthic (R-value of −0.278; $p > 0.05$) nor in the epibenthic assemblage in July (R-value of 0.222; $p > 0.05$) and October (R-value of −0.111; $p > 0.05$) (Fig. 3).

In total, we recorded 50 species in our experimental plots. In August 2007, we found 17 endobenthic species with a dominance of Annelida and Mollusca (Table 1). Number of endobenthic species in each treatment was 12 and no differences in the occurrence of single species between the treatments were detected (two-factorial ANOVA, $p > 0.05$ for all species).

The total number of epibenthic species was 33 with 19 macroalgae and 14 invertebrates in July and October 2007 (Table 2). In contrast to the endobenthic community, we detected effects of *S. muticum* on epibenthic species occurrence. *S. muticum* density significantly affected epibenthic species number in July (two-factorial ANOVA, $F_{3/13} = 11.02$, $MS = 10.24$, $p = 0.001$) (Fig. 4). Mean associated species number of oyster plots without *S. muticum* (23.4 ± 1.1) was significantly higher than of plots with a *S. muticum* density of 15 ind. m^{-2} (20.6 ± 1.3; Tukey's test, $p = 0.015$) and of 45 ind. m^{-2} (20.0 ± 1.3; Tukey's test, $p = 0.008$). Additionally, we detected a significant difference between the mean species number of the treatment with 7 *S. muticum* ind. m^{-2} (22.40 ± 0.89) and the one with 45 ind. m^{-2} (Tukey's test, $p = 0.008$). In October, however, no significant effect of *S. muticum* density on species number was detected (two-factorial ANOVA, $F_{3/13} = 1.31$, $MS = 4.46$, $p = 0.313$).

The mean total percentage coverage of all epibiont species oyster^{-1} was also significantly affected by *S. muticum* density in

Table 1
List of endobenthic species detected in experimental treatments of different *Sargassum muticum* densities (ind. m^{-2}) in August 2007.

Species	0	7	15	45
Nemertea				
Nemertini unidentified	p	p		p
Lineus ruber (Müller)	p		p	
Annelida				
Aricidea minuta (Southward)	c	p	p	p
Capitella capitata (Fabricius)	c	c	c	c
Eulalia viridis (Linné)			p	p
Malacoceros fuliginosus (Claparède)	c	c	c	c
Nereis diversicolor (O. F. Müller)		p	p	
Phyllodoce mucosa (Oersted)	p			
Scoloplos armiger (O. F. Müller)	p	p	p	p
Tharyx killariensis (Southern)	a	a	c	a
Tubificoides benedii (d' Udekem)	d	d	d	d
Tubificoides pseudogaster (Dahl)	d	d	d	d
Tubificoides sp.	d	d	c	d
Mollusca				
Mya arenaria (Linneus)		p		p
Mysella bidentata (Montagu)			p	
Macoma balthica (Linneus)	p			
Venerupis sp.		p		p
Total number of endobenthic species 17	12	12	12	12

Semi-quantitative data on species abundances are given as mean individual counts per 98 cm^3: p) present <1, c) common 1–5, a) abundant 6–10, d) dominant >10.

Table 2
List of sessile species detected in experimental treatments of different *Sargassum muticum* densities (ind. m^{-2}) in July and October 2007.

Species	July				October			
	0	7	15	45	0	7	15	45
Algae								
Chlorophyta								
Bryopsis lyngbyei Hornem.	p	p	p	p	p	p	p	p
Chaetomorpha aerea (Dillwyn) Kützing			p					
Enteromorpha spp. Link	p	p	c	p	p	p	p	p
Ulva spp.	p	p	p	p				
Phaeophyta								
Ectocarpus spp. Lyngb.	p	p	p	p	p	p	p	p
Elachista fucicola (Velley) Aresch.	a	a	c	c				
Petalonia fascia (O.F.Müll.) O. Kuntze	c	c	a	a	p	p	p	p
Sargassum muticum (Yendo) Fensholt					c	c	c	c
Rhodophyta								
Acrochaetium spp. Nägeli	p	c	c	p				
Antithamnion plumula (Ellis) Thur. In Le Jolis	c	c	c	p	c	c	c	p
Chondrus crispus Stackhouse	p	c	p	p	p	p	p	p
Ceramium nodulosum (Lightf.) Ducluz.	p	p	c	p	p	p	p	p
Dumontia incrassata (O.F. Müll) Lamour	p				c	p	p	p
Erythrotrichia spp.	p		p					
Polysiphonia nigrescens (Huds.) Grev.	d	a	a	a	c	c	c	p
Polysiphonia violacea (Roth) Spreng.	c	c	c	p	p	p	p	p
Polysiphonia elongata (Huds.) Spreng.	c	c	c	p	p	p	p	p
Porphyra sp.		p	p					
Fauna								
Porifera								
Halichondria panicea (Pallas)	p	p	p		c	c	c	p
Cnidaria								
Clytia hemispherica (L.)	p							
Obelia longissima (Pallas)	p	p	p	p	p	p	p	p
Obelia geniculata (L.)	p							
Sagartiogeton undatus (Müller)	a	a	a	a	p	p	p	p
Sarsia tubulosa (M.Sars)	p		p	p	p	p	p	p
Ciliophora								
Vorticella sp.	p	p	p	p	p	p	p	p
Mollusca								
Crepidula fornicata (L.)	c	c	c	c	p	c	c	c
Lepidochitonia cinerea (L.)	p	c	p	p	p	p	p	p
Crustacea								
Elminius modestus Darwin	a	a	c	c	d	d	a	a
Balanus crenatus Bruguière	d	d	d	d	a	a	a	c
Semibalanus balanoides (L.)	p	p	p	p	p	p	p	p
Balanus improvisus Darwin	p	p	p	p	p	p	p	p
Tunicata								
Molgula manhattensis (de Kay)	p	p	p	p	p	p	p	p
Styela clava Herdman		p			p	p	p	p
Total number of epibenthic species 33	29	26	28	24	25	24	25	25

Semi-quantitative data on mean species occurrence are given as: p) present: <1% cover oyster^{-1}; c) common: 1–5%; a) abundant: 6–9% and d) dominant ≥10%.

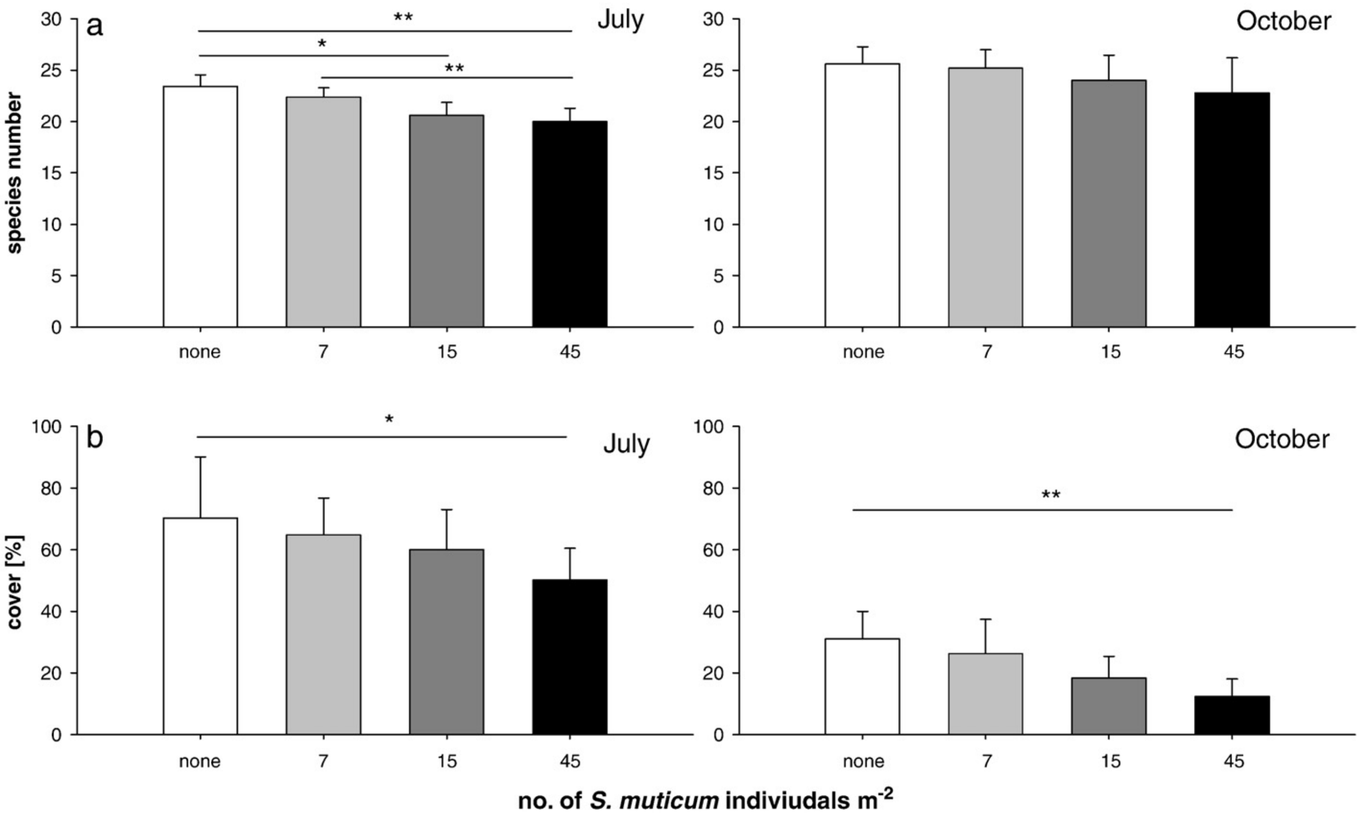

Fig. 4. Mean species number with standard deviation (+SD) (a) and mean percentage coverage (+SD) of all epibenthic species (b) at different *Sargassum muticum* densities in July and October. Significant differences are denoted as asterisks ($p<0.05$*, $p<0.01$**).

both July (two-factorial ANOVA, $F_{3/13}=8.47$, MS = 217.21, $p=0.002$) and October ($F_{3/13}=4.43$, MS = 265.21, $p=0.024$) (Fig. 4). The overall coverage was significantly reduced in plots with a *S. muticum* density of 45 ind. m^{-2} compared to the treatment without *S. muticum* (Tukey's test for July, $p=0.011$; and for October, $p=0.001$). In July, total mean coverage of epibenthic organisms oyster^{-1} decreased with increasing algal density from 70.2% in the treatment without *S. muticum* to 50.1% in plots with a *S. muticum* density of 45 ind. m^{-2} (Fig. 4). A similar pattern was found in October with a decreasing total mean coverage oyster^{-1} from 31.1% (without *S. muticum*) to 12.3% (*S. muticum* density of 45 ind. m^{-2}).

3.2. Species responses

Considering species level we found a significant effect of *S. muticum* density on the percent coverage oyster^{-1} of the three most abundant understorey algal species (Fig. 5). The mean coverage oyster^{-1} of *Polysiphonia nigrescens* (Hudson) Greville ex. Harvey was affected by *S. muticum* and significantly lower within the treatments with *S. muticum* than without in both July (two-factorial ANOVA, $F_{3/13}=10.72$, MS = 0.08, $p=0.001$) and October (two-factorial ANOVA, $F_{3/13}=3.90$, MS = 0.030, $p=0.034$). *P. nigrescens* showed the highest percent coverage of all algal species identified.

In July, the coverage of *Antithamnion plumula* (J.Ellis) Thuret was also impaired by *S. muticum* and appeared to decrease with increasing *S. muticum* density (two-factorial ANOVA, $F_{3/13}=4.05$, MS = 0.11, $p=0.031$). Percentage coverage oyster^{-1} was significantly different between the treatment without *S. muticum* and the treatment with a *S. muticum* density of 45 ind. m^{-2} (Tukey's test, $p=0.045$). No significant differences could be observed in October.

Further, percentage coverage oyster^{-1} of the brown alga *Elachista fucicola* (Velley) Aresch. was reduced within the treatments with *S. muticum* and showed a decreasing trend with increasing *S. muticum* densities in July (two-factorial ANOVA, $F_{3/13}=6.76$, MS = 0.14, $p=0.005$). We detected a significant difference in *E. fucicola* coverage between the treatment without and with 45 individuals m^{-2} of *S. muticum* (Tukey's test $p=0.013$) (Fig. 5). Additionally, we recognized a significant coverage difference of *E. fucicola* between the treatment with seven *S. muticum* m^{-2} and 45 individuals m^{-2} (Tukey's test $p=0.031$).

Decreasing native algal coverage over the treatments with increasing *S. muticum* density per plot was also observed in the species *Chondrus crispus* Stackh. and *Dumonita contorta* (Gmel.) Ruprecht. However, coverage in comparison to the above mentioned macroalgae was low. Mean coverage was <1.5% oyster^{-1} in the treatment with no *S. muticum* (treatment in which they achieved highest coverage) and, thus, we decided not to test statistically.

Considering sessile faunal organisms, the most abundant species were the barnacles *Balanus crenatus* Bruguière and *Elminius modestus* Darwin. Decreasing numbers in abundance oyster^{-1} for both species were observed between the treatments of increasing *S. muticum* density in July as well as in October (Table 3). However, results were not significant. Recruitment of all other sessile invertebrate species was also not significantly affected by *S. muticum.*

3.3. Water flow and sedimentation measurements

The relative water flow velocity was indirectly quantified by measuring weight loss of gypsum muffins. The density of *S. muticum* significantly affected water flow velocity (two-factorial ANOVA, $F_{3/13}=5.71$, MS = 21.75, $p=0.010$). Within the treatment without *S. muticum* water flow velocity was highest and significantly different from the treatment with 45 *S. muticum* individuals m^{-2} which showed the lowest water flow velocity (Tukey's test, $p=0.004$) (Fig. 6).

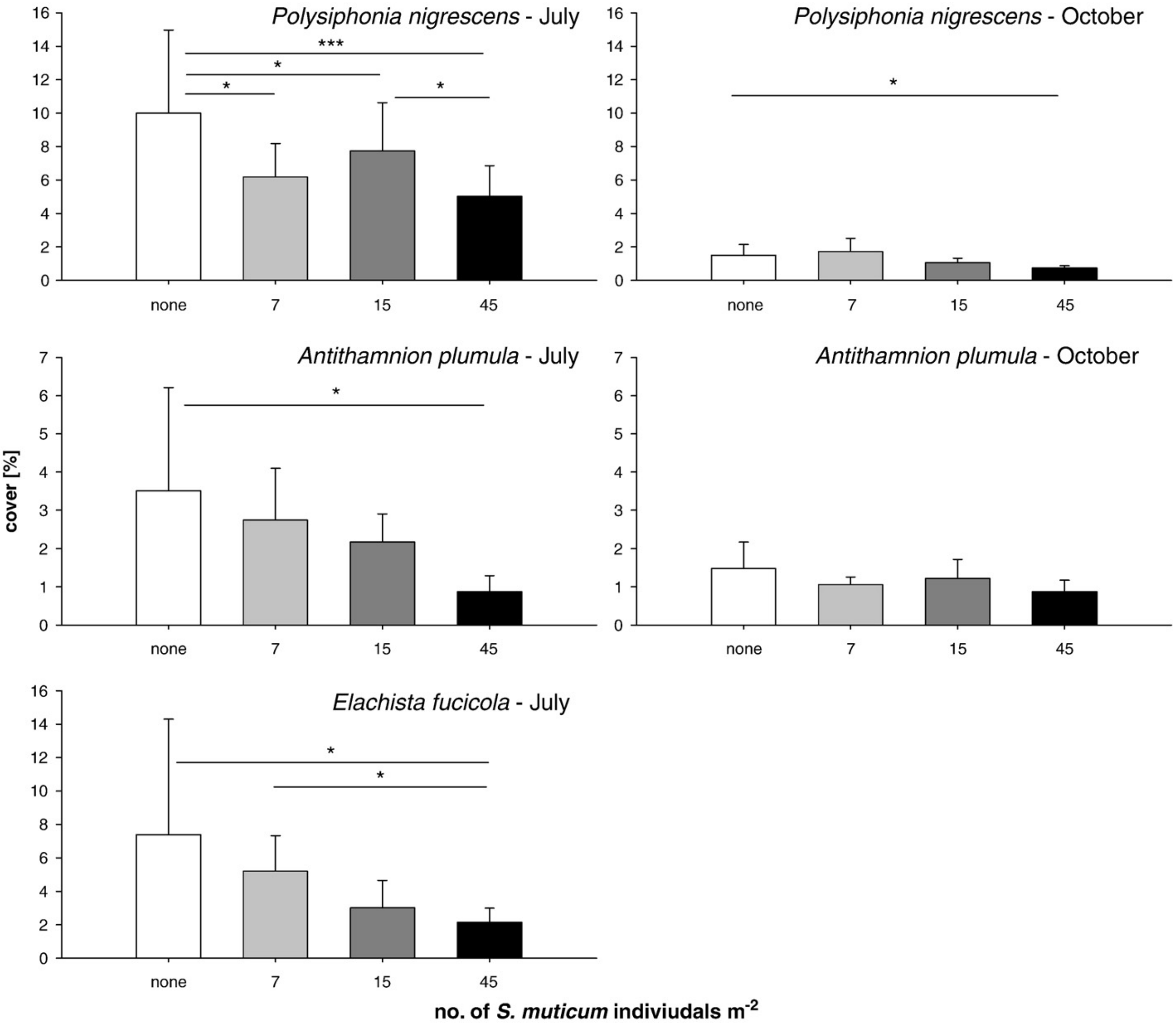

Fig. 5. Effects of manipulated *Sargassum muticum* density on percent coverage oyster^{-1} of understorey native algal species. Given are means with standard deviation (+SD). Significant results of the post-hoc Tukey test are denoted as asterisks ($p<0.05$*, $p<0.01$**, $p<0.001$***).

We could not find any differences in sedimentation rate between the treatments of different *S. muticum* densities (Fig. 6). Neither the mean overall accumulated material per sediment trap (two-factorial ANOVA, $F_{3/13}=0.76$, MS = 271.82, $p=0.54$) nor a single sediment fraction of a certain grain size showed significant differences.

4. Discussion

Using a small-scale field experiment we investigated the effects of the invasive brown alga *S. muticum* on benthic organisms associated with experimental oyster plots in the sedimentary environment of the Wadden Sea. There were no significant effects of the *S. muticum* canopy on community level. Additionally, no significant effects were observed on the infauna. However, we detected significant effects of *S. muticum* abundance on native understorey algae.

4.1. Effects of S. muticum on endobenthic organisms

A *S. muticum* canopy could have an impact on endobenthic organisms mediated by the change of physical factors. More specifically: the

Table 3
Mean densities oyster^{-1} (±SD) of the barnacles *Balanus crenatus* and *Elminius modestus* on experimental oyster reefs covered by different abundances of *Sargassum muticum* (ind. m^{-2}) in July and October 2007.

	July				October			
	0	7	15	45	0	7	15	45
Balanus crenatus	82.5 ± 45.3	65.5 ± 20.2	68.5 ± 28.9	65.8 ± 19.8	25.1 ± 12.4	20.7 ± 5.2	18.0 ± 9.2	11.9 ± 3.1
Elminius modestus	28.7 ± 7.8	33.6 ± 13.3	21.0 ± 8.1	17.9 ± 7.1	61.1 ± 12.4	49.9 ± 31.3	32.5 ± 14.1	28.9 ± 19.4

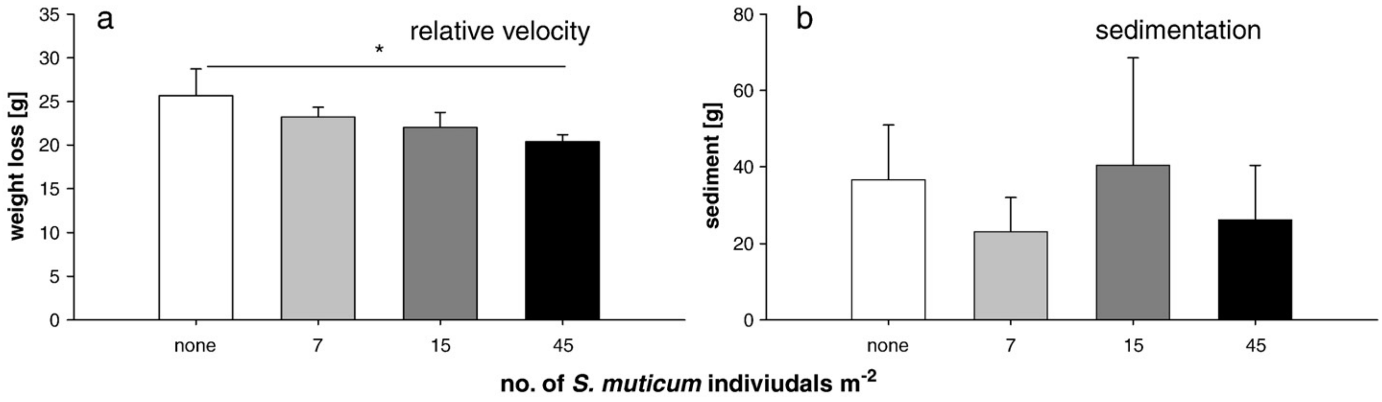

Fig. 6. Effects of manipulated *Sargassum muticum* density on water velocity measured as mean weight loss (+SD) of exposed gypsum muffins (a) and on mean sedimentation (+SD) (b). Significant results of the post-hoc Tukey test are denoted as asterisks ($p<0.05^*$).

canopy can reduce water velocity and, thus, indirectly may enhance sedimentation. However, contradictory effects of macro-algal coverage on sedimentation are reported. Irving and Connell (2006) found reduced sedimentation beneath a canopy of Fucales. Eckman et al. (1989), by contrast, found greater rates of particle deposition beneath understorey kelps. In case of *S. muticum*, however, neither Britton-Simmons (2004), Strong et al. (2006) nor this study could detect any effect on sedimentation. An explanation that reduction of water velocity did not have any effect on sedimentation rate in our experiment could be the restricted plot area (1 m^2). Particles that are slowed down above the plot would need some time to descend in the water column during which they are still transported by the current and they may touch the ground somewhere outside the plot. However, we did not observe any changes in sedimentation and sediment composition in the surrounding area of the experimental plots.

In contrast to the impacts of *S. muticum* on rocky shore communities, investigations on the effects on soft-bottom communities are scarce. Strong et al. (2006) detected significant differences between the endobenthic assemblages underneath *S. muticum* canopy and those in adjacent uncovered areas. They attribute the observed changes in endobenthic assemblage to shading, flow suppression and temperature stratification. Our results, by contrast, revealed no effects of *S. muticum* canopy on infauna. In accordance to the results of Strong et al. (2006) this pattern can be explained by the experimental time period which was restricted to four months. However, Albrecht and Reise (1994) also show that the infauna associated with mussel beds of *M. edulis* in the Wadden Sea was not affected by a heavy coverage with the bladder wrack *Fucus vesiculosus* forma *mytili* (Nienburg) despite of an increased sedimentation rate. It is likely that the endobenthic organisms are more affected by the bivalves lying directly at the sediment surface than by the algal coverage above the bivalve beds. Görlitz (2005) and Kochmann et al. (2008), for example, show that aggregations of blue mussels *M. edulis* beds and oysters *C. gigas* have different effects on the endobenthic community indicating that endobenthic organisms are strongly influenced by the kind of bivalve species at the sediment surface.

4.2. Effects of S. muticum on sessile epibenthic organisms

Although we detected a significantly reduced species number of epibionts on oyster beds as an effect of *S. muticum* coverage in July 2007 (but not in October) our results indicate that the differences in composition of an epibenthic soft-bottom oyster bed community in the Wadden Sea are small. However, we recognized a decrease of the mean overall coverage of sessile species on oyster beds with *S. muticum* in both July and October 2007 which is caused by a reduction of native macroalgae. No significant effect on the abundance of sessile benthic invertebrates could be detected.

The effect of *S. muticum* canopy on the coverage of native macroalgae was significant for three abundant species: *P. nigrescens*, *A. plumula* (both Rhodophyta) and *E. fucicola* (Phaeophyta). The overall trend was similar: the percentage cover decreased with increasing *S. muticum* density. Negative effects of *S. muticum* canopy on abundance of native understorey algae in subtidal habitats was also found by Curiel et al. (1998) in the Mediterranean, by Staehr et al. (2000) in the North Sea and by Britton-Simmons (2004) in the eastern Pacific.

The red macroalga *P. nigrescens* was the most dominant understorey algal species on the experimental oyster plots and was strongly affected by increased *S. muticum* densities in both July and October. Similarly, Curiel et al. (1998) and De Wreede (1983) report negative effects of a *S. muticum* canopy on otherwise dominant species of the order Ceramiales, Rhodophyta. Interestingly, Buschbaum et al. (2006) found that *P. nigrescens* grows as an epiphyte on *S. muticum* that may outweigh the reduction of P. *nigrescens* attached to *C. gigas*. However, in contrast to the oysters, *S. muticum* only represents an ephemeral habitat because the thalli break off in autumn and float away together with its associated species community.

The high occurrence of *E. fucicola* attached to oyster shells was not expected because this species is generally described as an epiphytic macroalga mainly growing on *Fucus*-species. However, Kornmann and Sahling (1977) found that *E. fucicola* may also be very abundant on other substrates in the Wadden Sea. In October, *E. fucicola* was not found because its main growing season is limited from April to August in the area (Kornmann and Sahling, 1977).

Reasons for algal coverage reduction below the *S. muticum* canopy could be changes in physical factors. The detected reduction in water flow is unlikely to result in a difference of nutrient availability between treatments because of the restricted plot size of 1 m^2 in our experiment. Additionally, Britton-Simmons (2004) found no effect of *S. muticum* on nutrient availability for understory algae. Critchley et al. (1990a) recognized a temperature stratification caused by the *S. muticum* canopy. However, incidental water temperature measurements revealed no differences inside and outside *S. muticum* aggregations in our experimental plots. One important factor causing effects on other algae may be the reduction of light by *S. muticum* coverage and the importance of the shading effect of *S. muticum* canopy was assumed by several authors (Curiel et al., 1998; Critchley et al., 1990a; Britton-Simmons, 2004; Strong et al., 2006; Domisch, 2008). Similar to their results casual light measurements in our experiment showed that beneath *S. muticum* canopy light was less than 5% of the uncovered plot at the same water depth. Since *S. muticum* is a pseudoperennial species with only the holdfast persisting through the year the shading effect is restricted to spring and summer (Norton, 1977). However, this is also the main growing season for most native macroalgae occurring in the area.

As shown for native macroalgae, *S. muticum* may also affect sessile benthic invertebrates recruiting and living below its canopy by mechanical disturbance of sweeping algal fronds (Jenkins et al., 1999; Leonard, 1999; Connell, 2003) and reduction in light and water flow. A light reduction favours the settlement of many invertebrate larvae that become photonegative at the end of their larval phase (Duggins et al., 1990; Connell, 2003). Additionally, by the suppression of water flow a depositional environment may emerge under the canopy where larval settlement is facilitated (Eckman et al., 1989; Leonard, 1999). Another important effect which acts more indirectly is the enhanced consumer pressure caused by the hiding opportunities beneath a canopy (Bertness et al., 1999). However, we obtained no data about predator abundance on the different plots. All these mentioned possible effects caused by *S. muticum* seem to be of less importance on oyster beds in the sedimentary environment of the Wadden Sea because *S. muticum* canopy did not affect the abundance of benthic sessile invertebrates. Similar results were obtained by Britton-Simmons (2004) who found no influence of a subtidal *S. muticum* canopy on benthic invertebrates at the Pacific coast of North America.

4.3. Conclusions

The introduction of *S. muticum* to the Wadden Sea and its occurrence on soft-bottom oyster beds may cause different effects. Epibenthic and endobenthic community composition at oyster aggregations seem to be not affected while single native algal species show a decrease in abundance. Additionally, *S. muticum* provides habitat for a rich epibiont species community associated with the algal thalli (Buschbaum et al., 2006). The ongoing dispersal of *C. gigas* and its spread into the shallow subtidal zone of the Wadden Sea result in a marked augmentation of biogenic hard substrate in an environment otherwise dominated by unstable sediments. This expansion may partly counterbalance the loss of highly diverse algae and invertebrate communities associated with subtidal native oyster (*Ostrea edulis* L.) and blue mussel beds (*M. edulis* L.) which were strongly overfished and disappeared from the Wadden Sea area in the second half of the 20th century (Hagmeier and Kändler, 1927; Saier et al., 2002; Cadée, 2007). Especially native macroalgae could strongly profit from the new oyster reefs because they provide an additional substratum for attachment. However, these structures are also used by the hitchhiking invader *S. muticum*. Dense canopies of *S. muticum* may reduce the establishment and occurrence of native macroalgae and may, therefore, limit the facilitative effect of Pacific oyster beds on native algae in the shallow subtidal zone. The invasion process of *S. muticum* is still ongoing and in summer 2009 we observed densities up to 50 *S. muticum* individuals m^{-2} attached to oyster beds in the shallow subtidal zone (Buschbaum and Reise, unpublished data) indicating that densities used in our experiments represent the current natural situation. However, due to the dynamic process of *S. muticum* invasion in the Wadden Sea we assume a further increase of its densities which could amplify the ecological effects on native species found in our study.

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