Artificial structures in sediment-dominated estuaries and their possible influences on the ecosystem

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ABSTRACT

Artificial substrates are omnipresent today in most estuaries mostly in form of massive rip-rap used for groynes and jetties. In the Weser estuary, Germany, 60% of the shoreline is covered with such artificial substrates while, natural rocky substrate is lacking, as in all Wadden Sea estuaries. This large quantity of artificial substrates may be colonized by a benthic hard-substrate community which differs from the local natural soft-substrate assemblage. In this study we examined species compositions, abundances, biomass, and numbers of species of subtidal benthic communities on groynes and in the natural habitat, the sediment, along the salinity gradient of the Weser estuary. Species composition changed on both substrates significantly with salinity and was also significantly different between the substrates. In a comparison with the sediment, the groynes did not provide any benefit for non-indigenous nor for endangered species in terms of abundance, biomass, and number of species, but represent habitats with higher total abundances and biomass; though some non-indigenous species even occurred exclusively on groynes. In particular, groynes supported filter-feeding organisms which play an important role by linking benthic and pelagic food webs. The dominance of the suspension feeders affects crucial estuarine ecosystem services and may have important implications for the estuarine management by altering the estuarine ecological quality status. Hence, artificial substrates should be considered in future conservation planning and in ecological quality monitoring of the benthic fauna according to the European Water Framework Directive.

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1. Introduction

Estuaries belong to the most productive environments worldwide, and their net primary production was estimated to equal almost that of tropical rain forests (up to 2000 g m^{-2} yr^{-1}; Whittaker and Likens, 1973). Their average productivity is more than twice as high as that of agricultural cropland (650 g m^{-2} yr^{-1}; Whittaker and Likens, 1973). Although only 5.8% of all coastal areas are estuaries, which corresponds to 0.35% of all habitats worldwide (values calculated using the information given by Costanza, 1997), they are of high value for many ecosystem functions and services. For example, the annual benefit provided by estuaries for human welfare is estimated alone for nutrient cycling at 21,100 US$ ha^{-1} yr^{-1} (Costanza, 1997), the highest estimate in their study which ranks before all seagrass and algae beds combined (19,002 US$ ha^{-1} yr^{-1}). Likewise, water filtration by estuarine mussels and clams is an important ecosystem service (Coen et al., 2007; Barbier et al., 2011). For example, laboratory studies have indicated that mussel filtration can significantly decrease chlorophyll-*a* concentrations (e.g. Granéli et al., 1993; Prins et al., 1995), and thus control phytoplankton biomass within the estuarine water column (Dame, 1996). Consequently, estuaries deserve to be protected not only because they support a small but unique habitat for a variety of brackish-water species.

Human influences on estuaries such as exploitation, habitat degradation, and pollution have been present for several thousands of years, but they intensified over the last centuries resulting in depletion of important species and habitats (Lotze et al., 2006). Today, estuaries in industrialized countries are probably among the most anthropogenically altered aquatic systems (Blaber et al., 2000) and are susceptible to numerous and strong pressures. The

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human influences on estuaries include many activities which are connected with their use as important shipping routes, like the straightening and deepening of navigation channels (e.g. Reise, 2005), the construction of jetties and groynes to increase and canalize flow, and to prevent sedimentation (Reise, 2005), as well as waterway-maintenance dredging (Ceia et al., 2013; Robinson et al., 2005) and dumping of dredged material (Bonvicini pagliai et al., 1985; Diaz and Rosenberg, 1995; Powilleit et al., 2009; Taupp and Wetzel, 2013). In addition, sediment pollution, as a legacy of industrialization, also has a high potential to influence estuarine biota at different trophic levels (Wetzel et al., 2013).

The urgent need to protect the valuable aquatic environments, including the marine, coastal, and estuarine environments, was recognized by the European Union policy and has resulted in several directives like the Habitats Directive (EEC, 1992), the Water Framework Directive (WFD; EC, 2000), and the Marine Strategy Framework Directive (MSFD; EC, 2008). All these directives explicitly demand monitoring programmes to identify the ecological quality status (EQS) and possible pressures. However, to execute these demands, broad knowledge about the habitats and their species inventory as well as detailed descriptions of important system components is essential. So far, only soft-substrate habitats have been included in the identification of the estuarine EQS (e.g. Borja et al., 2000; Rosenberg et al., 2004; Dauvin and Ruellet, 2007) while hard-substrate depending benthos has been largely neglected. This is surprising in the light of the fact that the fauna on hard substrates is usually more diverse (Bustamante et al., 2007), because artificial hard-substrate habitats are characterized by reduced predation and competition due to the ample availability of space (Connell, 2001; Airoldi et al., 2005; Bulleri and Airoldi, 2005; Glasby et al., 2007; Reise et al., 2006).

Estuaries may contain a wide range of different habitats in varying quantities like soft substrate, geologically derived rocky reef structures, and mussel beds. All these habitats have their own specific substrate characteristics which largely determine invertebrate species composition. Only two studies on the sublittoral benthic fauna of the Weser estuary have been performed yet. Dittmer (1981) and Gosselck et al. (1993) gave a species inventory of certain subtidal benthic communities. The artificial hard-substrate has not been described so far. Geologically derived hard-substrate, such as stones and pebbles is very rarely found in the estuaries of the Wadden Sea, because the recent deposits following the last ice age (12,000 years ago) are free of stoney material (Behre, 2004). In the Weser estuary it is highly assumed that besides the sediment biologically derived hard substrate occur, such as sublittoral mussel beds formed by the blue mussel *Mytilus edulis*, though no studies have been published so far in this regard. These biogenic structures form an important habitat as they enable other organisms to settle on these structures, such as macroalgae (Lang and Buschbaum, 2010) and invertebrates (Buschbaum et al., 2009), and thus increase overall diversity, abundance, and biomass (Dittmann, 1990) in an environment where hard substrates originally not exist. Consequently, they play an important role in regulating macrofaunal diversity in soft bottom habitats (Commito et al., 2008) and promote the development of complex trophic and competitive interactions (Dittmann, 1990).

Steel pilings, jetties, and groynes are common habitats in most estuaries today. Estimates (Reznichenko, 1978; cited in Railkin, 2004) predicted the total surface of all artificial materials and structures in marine environments to sum up to 5000 km². We can readily assume that this value has increased since Reznichenko (1978) published his estimates, and that a large share is located in estuaries of industrialized countries. In the Weser estuary, about 60% of the shoreline is covered with artificial substrates (Schuchardt et al., 1984).

Community compositions on artificial hard substrates differ usually from that on natural rocky substrates and are not just a simple copy thereof (e.g. Andersson et al., 2010; Guerra-García et al., 2004; Marzinelli et al., 2009). The presence of hard-bottom fauna on artificial substrates can influence the established community composition on adjacent soft substrates (Davis et al., 1982; Grant et al., 1995; Krone et al., 2013; Seitz et al., 2006). When non-indigenous species (NIS) occur on artificial structures (Ruiz et al., 2009; Glasby et al., 2007; Tyrrell and Byers, 2007; Wasson et al., 2005) these substrates may serve as stepping stones for invasive alien species (Apte et al., 2000; Wilhelmsson and Malm, 2008). Commercial ports and recreational marinas therefore provide the first habitats in a colonization corridor for introduced species (Floerl and Inglis, 2005; Bulleri and Airoldi, 2005). However, artificial substrates were also found to present refuges for endangered species of crustaceans (Krone and Schröder, 2011) or limpets (García-Gómez et al., 2010).

Threatened and endangered species are often listed in the so-called 'Red Lists'. The Red List of macrofaunal benthic invertebrates of the Wadden Sea (Petersen et al., 1996) uses different classifications to represent the potential level of extinction. The classification 'endangered' means that this species has shown a significant and continuous decline in abundance over a period of at least 10 years and that a real threat exists that this species faces extinction. 'Vulnerable' indicates species, which may be still relatively abundant locally, but of which a decline has been observed in the past 10 years in the entire area. 'Susceptible' assumes a threat of unknown degree. For the full classification scheme see von Nordheim et al. (1996).

Despite extensive studies of artificial substrates in Australian estuaries and in European and American coastal waters (see papers on seawalls, pilings and pontoons by Chapman, 2006; Dafforn et al., 2012; Firth et al., 2014; Glasby et al., 2007; Perkol-Finkel et al., 2012; Pister, 2009; Wasson et al., 2005; etc.), studies on fouling communities on artificial substrates in the Wadden Sea estuaries are still lacking. Consequently, it is the specific aim of this study to quantitatively describe the fouling communities on artificial structures (groynes) along the salinity gradient of the Weser estuary, Germany, in comparison with the natural local habitat, the sediment. We hypothesized that groynes had higher total benthos abundance, biomass, and number of species than the surrounding sediment (cf. Bastrop et al., 1997; Ricciardi and Bourget, 1999). We also proposed that benthic species composition on the groynes differs from sediment dwelling benthos (cf. Bastrop et al., 1997) and that both communities change over the estuarine salinity gradient (cf. Boesch, 1977; Dittmer, 1981; Mannino and Montagna, 1997; Ysebaert et al., 2003). Significant differences in species assemblages between the substrates 'groyne' and 'sediment' would suggest that the EQS of estuaries should not be determined solely with the sediment benthos. In addition, we expected that species, which are considered endangered, show higher abundances and have higher numbers of species on artificial substrates (García-Gómez et al., 2010; Krone and Schröder, 2011; Perkol-Finkel et al., 2012). Likewise, we expected NIS to occur on the groynes in higher abundances with higher species numbers (cf. Ruiz et al., 2009; Glasby et al., 2007; Tyrrell and Byers, 2007; Wasson et al., 2005). We also expected that groynes support more suspension feeders, in particular mussels, in terms of abundance and numbers of species (cf. Ricciardi and Bourget, 1999). This could affect water-column quality at least on a local scale. As we did not measure species-specific filtration rates, we used literature values to calculate the total filtration rate of blue mussels on the groynes and compared it with the mean annual river discharge volume to estimate the potential influence of this mussel population on the water quality.
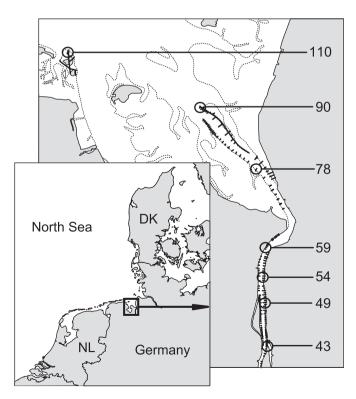
2. Material and methods

2.1. Study area

The Weser estuary that is located on the southern coast of the North Sea discharges the water of the River Weser (catchment 46,000 km[2]; Lange et al., 2008) into the Wadden Sea (Fig. 1), the largest coherent tidal-flat area in the world (Reise, 2005). The estuary is characterized by diurnal tides (the mean tidal range is about 3.8 m at the tidal gauge Alter Leuchtturm Bremerhaven, where the river opens its funnel-shaped mouth into the Wadden Sea (cf. Fig. 1; Lange et al., 2008). The mean water temperature ranges from approximately 5 °C in winter to 20 °C in summer, and the average discharge of the River Weser is 326 m^3 s^{-1} (Lange et al., 2008).

Within the estuarine funnel, the location and depth of the navigation channel is maintained by groynes, jetties, and guiding dykes, or to some extent by maintenance dredging. These structures accelerate the flow velocity of the tidal currents and serve as shore defences. Today, two guiding dykes and several groynes stabilize the navigation channel on both sides of the estuary (Fig. 1). As a consequence of these structures the cross section in the outer estuary was reduced to about 10–15% of its initial width (cf. Fig. 1). In the inner estuary, numerous groynes, usually built of massive rip-rap, spread on both banks of the river.

No information was available about the salinity distribution in the Weser estuary which might be used to identify salinity zones according to the Venice classification (Venice system, 1959). We obtained monthly longitudinal conductivity data of six years from 1995 to 2001, river-km 40–80, from the River Basin Community Weser. These conductivity values were converted to practical salinity unit values (PSU) according to the thermodynamic properties of seawater (IOC et al., 2010). To identify the different salinity zones in the Weser estuary and to identify their variability in the course of the year, we fitted average PSU lines to the four different seasons (April and May, June–August, September–November, and December–March) using a non-parametric method for estimating regression lines (LOESS procedure). LOESS lines were computed with the 'loess' function provided in R (R Development Core Team, 2013). The intersections of these lines with the different salinity zones (oligohaline = 0.5–4 PSU, mesohaline = 5–18 PSU, polyhaline = 18–30 PSU, and euhaline > 30 PSU) were used to identify the zones by the corresponding river-kilometres according to the Venice classification (Venice system, 1959).

Monthly salinity measurements over a six-year period from 1995 to 2001 showed a wide range across the estuary from river-km 40 to 80 (Fig. 2). Average values over different seasons showed that the borders of the salinity zones were located farther downstream in spring in the months April and May and winter in the months from December to March, while in summer in the months of June to August and even more in autumn in the months from September to November, this border is farther upstream. In general, the oligohaline zone extends from farther upstream at river-km <40 towards river-km 50 to 60 (5 PSU). The mesohaline zone with a salinity of 18 extends downstream to river-km 65–73, and the upper border of the polyhaline stretch with a salinity of 30 can be localized from river-km 75 to >80. Under extreme situations with extremely high or low river discharges, this pattern can be different, with the upper border of the oligohaline zone ranging between river-km 49 and 65 (cf. Fig. 2). Likewise, waters with salinities of 30 PSU can penetrate into the estuary upstream to river-km 63.

2.2. Data collection and processing

Groyne substrate was sampled on seven groynes along the estuary, from river-km 43 to km 110 (Fig. 1). At each groyne three samples were taken of the hard substrate and three from the adjacent sediment. Sampling depth was 2–3 m below the chart datum of nautical charts (Lowest Astronomical Tide, LAT). At each
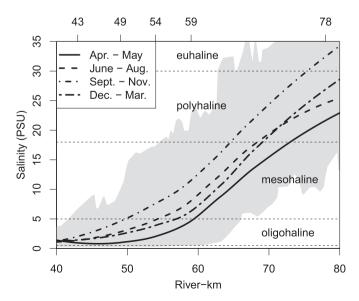

Fig. 1. The Weser estuary (German Bight, North Sea) with locations of groynes and longitudinal dykes (thick lines). The sampling stations are marked by circles and named with the official kilometre system of the lower River Weser (river-km). The dotted line corresponds to intertidal sand and mudflat areas. DK = Denmark, NL = The Netherlands.

Fig. 2. Seasonal distribution of salinity values (PSU) in the Weser estuary from the river-kilometres 40 to 80. Salinity classes according to the Venice classification (Venice System, 1959) are given. The grey polygon indicates the total range of salinity measurements. Sampling positions are indicated at the top.

groyne three samples were removed using a commercial hydraulic power-shovel excavator equipped with a clamshell. For each sample the fauna attached to the stones, equivalent to an area of 0.1 m^2 (stones were chosen at random), was scraped off and preserved in 70% ethanol. At each groyne, three soft-bottom samples were taken with the shovel excavator. However, at river-km 90 no sediment samples could be obtained because a sublittoral mussel bed surrounded the groyne. Because no studies have been published yet giving information of sublittoral mussel beds in the Weser estuary we collected two samples with a surface of 0.1 m^2. However, we included the samples from the mussel bed and the adjacent groyne only in our quantitative description, but did not use them in our statistical analysis. We used a box corer with 0.1 m^2 surface area to gain a subsample from each of the three shovel-excavator samples down to a depth of 20 cm. The sediment, i.e. homogenous sandy mud, was sieved through a 0.5 mm sieve, and the organisms were preserved in 70% ethanol. Faunal specimens of the substrates were sorted and counted under a dissection microscope and were identified to the lowest taxonomic level possible.

Species-specific biomass (i.e. ash-free dry weight; AFDW) was calculated as follows: specimens were placed at 100 °C in an oven for 12 h and afterwards cooled down to room temperature for approximately 4 h in a desiccator. Thereafter, the samples were weighed to determine the dry weight. They were reheated to 550 °C for 1 h, cooled down to room temperature in a desiccator for approximately 6 h and weighed to determine the ash content. The AFDW was calculated by subtracting the weight of the ash content from the dry weight. Though, we used ethanol for fixation of animals, the AFDW from our study is comparable with that of formalin-fixed samples (cf. Wetzel et al., 2005).

The feeding guilds, i.e. predator, scavenger, omnivore, deposit-, and suspension-feeder were assigned using the Biological Traits Information Catalogue (MarLIN, 2006) and the protection status of threatened and endangered species was determined according to the Red List of macrofaunal benthic invertebrates of the Wadden Sea (Petersen et al., 1996). NIS were assigned according to the national checklist for alien aquatic species in Germany (Gollasch and Nehring, 2006).

Total filtration of *M. edulis* was calculated for a 12 km stretch ranging from river-km 78 to 90. The total length of all groynes in this area was estimated from nautical charts, and the total abundance of sublittoral *M. edulis* was calculated. Total filtration performance was calculated using the filtration rates for *M. edulis* from the literature range from 1.5 to 3.0 l h^{-1} individual^{-1} (Mølenberg and Riisgård, 1979; Famme et al., 1986; Clausen and Riisgård, 1996).

2.3. Data analysis

Statistical analysis and figure compilation was performed using the R software (version 3.0.2; R Development Core Team, 2013). Samples collected from individual groynes are not independent, so that we calculated the mean values from the samples taken from the individual groynes and the adjacent sediments to avoid pseudoreplication (cf. Hurlbert, 1984). All further analyses were carried out with these mean values.

To test our hypotheses that artificial hard-substrates had higher total benthic abundance, biomass, number of species, higher abundance and number of NIS, higher abundance and number of threatened species, and higher abundance and number of suspension feeders, we performed analysis of covariance (ANCOVA) with substrate (*i.e.* artificial hard substrate *vs.* sediment) as independent variable and salinity as covariate (six salinity levels: 1.2, 2.3, 2.7, 6, 25.5, and 30 PSU). Interactions between the variables were explored and found to be not of significance for all dependent variables. We also calculated the effect sizes eta squared (η^2), the

ratio of the sum of squares for an effect to the total sum of squares. It can vary between 0 and 1 corresponding to 0 and 100% and indicates the relative degree to which the variance is associated with the effect (cf. Levine and Hullett, 2002). Prior to this analysis, data were checked for normal distribution by means of the Shapiro-test (significance level $\alpha = 0.05$; Shapiro and Wilk, 1965) and homogeneity of variances using the Fligner–Killeen test ($\alpha = 0.05$; Conover et al., 1981). Data were transformed to reach normal distribution by log$_{10}$ ($x + 1$)-transformation.

To test if benthic species composition on artificial structures differs from sediment dwelling benthos and if both communities change along the estuarine salinity gradient, we calculated a similarity matrix using the Bray Curtis similarity index (Kruskal and Wish, 1978) with double-square-root-transformed abundance data. A two-way permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001; McArdle and Anderson, 2001; maximum permutations = 999) was calculated using the 'adonis' function in the R-package 'vegan' (Oksanen et al., 2011) to test whether the species composition changed along the estuarine salinity gradient and if differences existed between the substrates 'groyne' and 'sediment'. Then, we used cluster analysis of mean values of abundance to display different species assemblages. Significantly different clusters were identified using the similarity profile routine (SIMPROF) for sample groups (Clarke et al., 2008). The SIMPROF test was calculated using the 'simprof' function from the R-package 'clustsig' (Whitaker and Christman, 2010). Further, we used analysis of similarity percentages (SIMPER; Clarke, 1993) to rank species contributing most to the average Bray–Curtis dissimilarities between different clusters. The SIMPER procedure was calculated using the 'simper' function from the R-package 'vegan' (Oksanen et al., 2011).
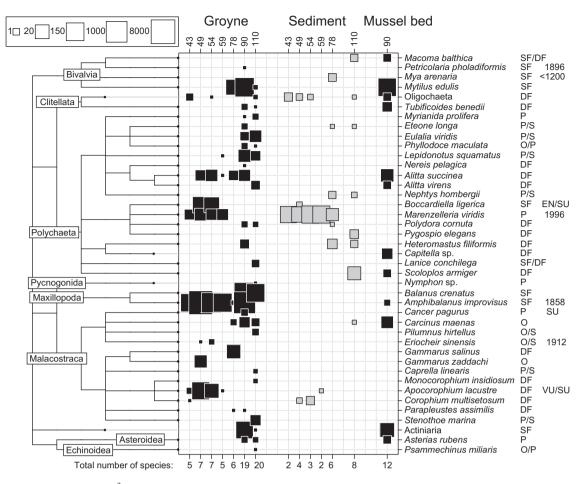
3. Results

3.1. Species composition

From the total 41 taxa found in our study 35 taxa occurred on groynes and 12 taxa could be found in the sediment (Fig. 3). On the groynes, 19 species were found exclusively there, while two species, *Nephtys hombergii*, *Mya arenaria*, were solely present in the sediment. The most abundant species on the groynes was *Amphibalanus improvisus* with mean abundances ranging from 160 individuals 0.1 m^{-2} at river-km 43 to 6667 individuals 0.1 m^{-2} at km 49. *Apocorophium lacustre* and *Boccardiella ligerica* were also very abundant on the groynes from river-km 43 to 59 with mean abundance values up to 133 and 64 individuals 0.1 m^{-2}, respectively. The sediment between river-km 43 and 78 was predominately populated by the annelid worm *Marenzelleria viridis* with mean abundances up to 104 individuals 0.1 m^{-2}. The same species was also present on groynes from river-km 43 to 59, however there, only mean abundances up to 11 individuals 0.1 m^{-2} could be found. In the single mussel bed, we found at river-km 90 the blue mussel *M. edulis* as the most abundant species with 176 individuals 0.1 m^{-2}. Other species present in the mussel-bed samples in higher mean densities were the annelid worms *Alitta succinea* with 14 individuals 0.1 m^{-2} and *Heteromastus filiformis* with 6 individuals 0.1 m^{-2}, and some not further identified sea anemones with 26 individuals 0.1 m^{-2}.

3.2. Community parameters

Regarding total mean abundance, a significant main effect was found for substrate, $F(1, 9) = 11.99$, $p = 0.007$, but not for the covariate salinity, $F(1, 9) = 5.1$, $p = 0.05$ (Table 1). The strength of the relationship between substrate and the mean abundance was

Groyne | Sediment | Mussel bed

1☐ 20☐ 150☐ 1000☐ 8000☐

43 49 54 59 78 90 110 | 43 49 54 59 78 110 | 90

Species	Feeding	Status
Macoma balthica	SF/DF	
Petricolaria pholadiformis	SF	1896
Mya arenaria	SF	<1200
Mytilus edulis	SF	
Oligochaeta	DF	
Tubificoides benedii	DF	
Myrianida prolifera	P	
Eteone longa	P/S	
Eulalia viridis	P/S	
Phyllodoce maculata	O/P	
Lepidonotus squamatus	P/S	
Nereis pelagica	DF	
Alitta succinea	DF	
Alitta virens	DF	
Nephtys hombergii	P/S	
Boccardiella ligerica	SF	EN/SU
Marenzelleria viridis	P	1996
Polydora cornuta	DF	
Pygospio elegans	DF	
Heteromastus filiformis	DF	
Capitella sp.	DF	
Lanice conchilega	SF/DF	
Scoloplos armiger	DF	
Nymphon sp.	P	
Balanus crenatus	SF	
Amphibalanus improvisus	SF	1858
Cancer pagurus	P	SU
Carcinus maenas	O	
Pilumnus hirtellus	O/S	
Eriocheir sinensis	O/S	1912
Gammarus salinus	DF	
Gammarus zaddachi	O	
Caprella linearis	P/S	
Monocorophium insidiosum	DF	
Apocorophium lacustre	DF	VU/SU
Corophium multisetosum	DF	
Parapleustes assimilis	DF	
Stenothoe marina	P/S	
Actiniaria	SF	
Asterias rubens	P	
Psammechinus miliaris	O/P	

Bivalvia
Clitellata
Polychaeta
Pycnogonida
Maxillopoda
Malacostraca
Asteroidea
Echinoidea

Total number of species: 5 7 7 5 6 19 20 | 2 4 3 2 6 8 | 12

Fig. 3. Mean abundances (individuals 0.1 m^{-2}; groynes and sediments: $n = 3$, mussel bed: $n = 2$) of all species found in the Weser estuary on groynes, in the sediments, and on a mussel bed adjacent to a groyne at km 90. Black squares indicate groynes and mussel bed, grey squares show sediment samples. The Red List status (EN = endangered, VU = vulnerable, SU = susceptible) according to Petersen et al. (1996) and non-indigenous species (indicated by the year of their first record in German waters) are indicated according to the national checklist for aquatic alien species in Germany (Gollasch and Nehring, 2006). Feeding types: P = predator, S = scavenger, O = omnivore, DF = deposit-feeder, SF = suspension-feeder. The samples from the mussel bed and the adjacent groyne were included in our quantitative description but were not used in the statistical analysis.

assessed by the effect size η^2. Substrate accounted for 46% of the variance in mean abundance (cf. Table 1). Mean abundance was always higher on the groynes, with values ranging from 69 individuals m^{-2} at river-km 78 to 6892 individuals m^{-2} at river-km 49 compared with sediments with values ranging from 16 individuals m^{-2} at river-km 78 to 106 individuals m^{-2} at river-km 54. Likewise, as to mean biomass, a significant main effect was found for substrate, $F(1, 9) = 6.13$, $p = 0.035$, but not for the covariate salinity, $F(1, 9) = 0.08$, $p = 0.79$, and substrate accounted for 40% of the variance in mean biomass. The mean biomass in the sediment samples ranged from 0.04 g AFDW 0.1 m^{-2} at river-km 78 to 0.16 g AFDW 0.1 m^{-2} at river-km 49, and the mean biomass on groynes ranged from 0.11 g AFDW 0.1 m^{-2} at river-km 43 to 24.4 g AFDW 0.1 m^{-2} at river-km 49. At river-km 49, the groyne was populated by a high number of the suspension-feeding barnacle A. improvisus. There, A. improvisus occurred with a mean abundance of 6667 individuals 0.1 m^{-2} and a mean biomass of 24.3 g AFDW 0.1 m^{-2}. The number of species showed a significant effect for substrate, $F(1, 9) = 9.05$, $p = 0.015$, and salinity, $F(1, 9) = 7.2$, $p = 0.025$, indicating that differences in number of species changed along the salinity gradient on both substrates. Both substrates showed the highest number of species at the outermost station at river-km 110 with the highest salinity of 30. There, the mean number of species was 11.3 species 0.1 m^{-2} on the groyne and 4.3 species 0.1 m^{-2} in the sediment, and the mean number of

species was always higher on the groynes than in sediments, except at river-km 78 (cf. Fig. 3). Substrate accounted for 36% of the variance in number of species and the covariate salinity for 29%.

3.3. Non-indigenous species

Altogether, five NIS could be identified in our study (cf. Fig. 3), of which the clams Petricolaria pholadiformis and M. arenaria were found only in low abundances in the sediment. P. pholadiformis was present with a mean abundance of <1 individuals 0.1^{-2} at river-km 90 and M. arenaria with a mean abundance of 2 individuals 0.1 m^{-2} at river-km 78. The Chinese mitten crab Eriocheir sinensis was only present on the groynes at river-km 49 and 54, and the barnacle A. improvisus occurred only in groyne samples. The annelid worm M. viridis, in contrast, was present on the groynes and in the sediment. The NIS P. pholadiformis, M. arenaria, A. improvisus, and E. sinensis have been part of the indigenous species communities at the German North Sea coast and in the estuaries for over 100 years and have been mentioned to occur here already in 1896, 1860, 1858, and 1912, respectively (cf. Gollasch and Nehring, 2006 and references therein). Only M. viridis is relatively new in the species pool, with first records in 1996 (Bastrop et al., 1997). Though some NIS species occurred only on the groynes such as the barnacle A. improvisus and E. sinensis and others were present only in the sediment like M. arenaria, we found for total abundance of NIS a

Table 1
Results of the ANCOVA testing for total abundance, total biomass, number of species, abundance of suspension feeders (SF), number of suspension-feeding species, abundance of non-indigenous species (NIS), number of non-indigenous species, abundance of Red List species (RL), and number of Red List species along the salinity gradient and between the substrates (groyne *vs.* sediment). Asterisks indicate significant differences at $p < 0.05$,*; $p < 0.01$,**; $p < 0.001$,***. In addition we give the effect size η^2.

		df	MS	F	p	η^2
Abundance	Salinity	1	5.67	5.10	0.05	0.20
	Substrate	1	13.33	11.99	0.007**	0.46
	Residuals	9	1.11			
Biomass	Salinity	1	0.06	0.08	0.79	0.01
	Substrate	1	4.56	6.13	0.035*	0.40
	Residuals	9	0.74			
No. of species	Salinity	1	0.68	7.20	0.025*	0.29
	Substrate	1	0.86	9.05	0.015*	0.36
	Residuals	9	0.09			
NIS abundance	Salinity	1	58.77	29.72	<0.001***	0.73
	Substrate	1	3.76	1.90	0.20	0.05
	Residuals	9	1.98			
No. of NIS species	Salinity	1	0.67	5.71	0.041*	0.37
	Substrate	1	0.09	0.81	0.39	0.05
	Residuals	9	0.12			
Red List abundance	Salinity	1	5.85	2.31	0.16	0.16
	Substrate	1	7.89	3.12	0.11	0.22
	Residuals	9	2.53			
No. of Red List species	Salinity	1	0.62	6.26	0.034*	0.32
	Substrate	1	0.40	4.10	0.07	0.21
	Residuals	9	0.10			
SF abundance	Salinity	1	0.81	0.50	0.50	0.01
	Substrate	1	89.07	54.80	<0.001***	0.85
	Residuals	9	1.63			
No. of SF species	Salinity	1	0.21	2.86	0.13	0.09
	Substrate	1	1.37	18.38	0.002**	0.61
	Residuals	9	0.07			

significant effect only for the covariate salinity, $F(1, 9) = 29.72$, $p < 0.001$, but not for substrate, $F(1, 9) = 1.9$, $p = 0.2$ (Table 1). This indicates that total NIS abundance changed significantly over the salinity gradient, but no significant differences were present between the groynes and the sediment. Salinity accounted for 73% of the variance in mean NIS abundance. NIS abundance on groynes was highest in the inner estuary at river-km 49 with 6677 individuals 0.1^{-2} and lowest in the outer estuary at river-km 78 with <1 individuals 0.1^{-2}. Likewise, the number of NIS species showed a significant effect for the covariate salinity, $F(1, 9) = 5.71$, $p < 0.041$, but not for substrate, $F(1, 9) = 0.81$, $p = 0.39$, indicating, that the number of NIS changed significantly along the salinity gradient, but no significant differences occurred between the groynes and the sediment. Salinity accounted for 37% of the variance in the number of NIS. The mean number of NIS was highest on the groyne at river-km 54 with 2.7 species 0.1^{-2} while no NIS were found on the groyne and in the sediment at river-km 110.

3.4. Threatened and endangered species

In our study, we found three species mentioned in the Red List of the Wadden Sea and the German coast (cf. Fig. 3). *B. ligerica* was present with abundances as high as 44—64 individuals 0.1 m^{-2} on the groynes and with abundances as low as 1 individual 0.1 m^{-2} in the sediment. This species is classified as 'endangered' over the entire Wadden Sea, but only 'susceptible' in the German part. *A. lacustre* which is described in the Red List as 'vulnerable' in the Wadden Sea and 'susceptible' in the German part was found exclusively on the groynes of the inner estuarine section at river-km 43—59. The crab *Cancer pagurus* — just a single individual was found on the groyne at river-km 90 — has been classified as 'susceptible' both in the Wadden Sea and the German part of the North

Sea. Though some threatened species such as *B. ligerica* occurred in higher abundances on the groynes or were restricted in their occurrence to this substrate. We found no significant main effect for substrate, $F(1, 9) = 3.12$, $p = 0.11$, and no significant effect for the covariate salinity, $F(1, 9) = 2.31$, $p = 0.16$ (Table 1), for total abundance of threatened species. This indicates that threatened species abundance was not significantly different between the groynes and the sediment, and no significant differences were present along the salinity gradient. For the total number of threatened species we also found no significant main effect for substrate, $F(1, 9) = 4.1$, $p < 0.07$, but for the covariate salinity, $F(1, 9) = 6.26$, $p = 0.034$, indicating that the total number of threatened species changed significantly along the salinity gradient, but no significant differences were present between the groynes and the sediment. Salinity accounted for 34% of the variance in the number of threatened species. Higher numbers and abundances of threatened species occurred in the inner estuarine section at river-km 43—59.

3.5. Feeding guilds

The discrimination of the benthic macrofauna into different feeding guilds showed a pronounced difference between the substrates. For feeding guild assignment see Fig. 3. On the groynes, from river-km 43 to 110, suspension-feeding species were the dominant feeding guild with total abundance values ranging between 43 individuals 0.1^{-2} at river-km 78 and 6730 individuals 0.1^{-2} at river-km 49. The suspension-feeders were *B. ligerica* in the inner estuarine section ranging from river-km 43 to 59, *A. improvisus* from river-km 43 to 90, *M. edulis* in the outer section from river-km 78 to 110, and sea anemones at river-km 90 and 110. The sediment was dominated by predators, mainly *M. viridis*, with abundance values ranging from 1 individual 0.1^{-2} at river-km 110 to 104 individuals 0.1^{-2} at river-km 54. The abundance of deposit-feeders in the inner estuarine section from river-km 43 to 59 ranged between <1 individuals 0.1^{-2} at river-km 59 and 138 individuals 0.1^{-2} at river-km 49. The remaining feeding guilds, the catholic feeders and the scavengers such as *Carcinus maenas*, *Pilumnus hirtellus*, *E. sinensis*, and *Gammarus zaddachi* were either totally absent, like at river-km 43, or present with abundances ranging between <1 individuals 0.1^{-2} at river-km 49 and 21 individuals 0.1^{-2} on the groyne at river-km 110. Regarding the total abundance of suspension feeders, we found a significant main effect for substrate, $F(1, 9) = 89.07$, $p < 0.001$, and no significant effect for the covariate salinity, $F(1, 9) = 0.5$, $p = 0.5$ (Table 1). Substrate accounted for 85% of the variance in abundance of suspension feeders. In terms of species number of suspension feeders, we also found a significant main effect for substrate, $F(1, 9) = 18.38$, $p = 0.002$, but no significant effect for the covariate salinity, $F(1, 9) = 2.86$, $p = 0.13$. Substrate accounted for 61% of the variance in the number of suspension feeding species. This indicates that the suspension feeders in the estuary are highly associated with the groynes.

3.6. Species composition

The PERMANOVA results (Table 2) indicate a significant change in the species assemblages along the estuarine gradient and between the substrates, 'groyne' and 'sediment'. Moreover, the interaction term was also significant indicating that the species assemblage of the groynes and that of the sediments change differently along the estuarine gradient.

Cluster analysis (Fig. 4) showed a clear distinction between the inner estuarine section ranging from river-km 43 to 78 and the outer estuarine section ranging from river-km 78 to 110, regardless of substrate. This distinction follows roughly the salinity

Table 2
Results of the two-way PERMANOVA testing for differences in the benthic community composition along the estuarine salinity gradient, between the substrates (groyne *vs.* sediment), and possible interactions. *Asterisks* indicate significant differences at $p < 0.01$,**; $p < 0.001$,***.
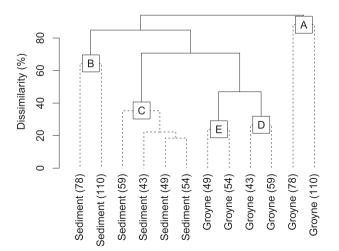
	df	MS	F	r^2	p
Salinity	1	0.79	3.70	0.17	0.002**
Substrate	1	1.27	5.90	0.28	0.001***
Salinity × Substrate	1	0.75	3.50	0.17	0.003**
Residuals	8	0.23			

classification (cf. Fig. 2) with the mesohaline stretch ranging from approximately river-km 55 to 69. Differences between substrates are pronounced in both sections. The SIMPROF procedure indicates five significantly different clusters (Fig. 4). Cluster A consists of the samples of the groynes from river-km 78 to 110, cluster B contains the sediment samples from river-km 78 to 110, and cluster C is described by the sediment samples from the inner estuarine section. The groynes of the inner estuarine section are divided into the two clusters D and E.

Analysis of similarity percentages showed that the species contributing most to the differences between the substrates 'groyne' *vs.* 'sediment' in the outer estuary from river-km 78 to 110 were *M. edulis* with a contribution of 9.2% to the observed differences and *Balanus crenatus* with 6.1% (Table 3). In the inner estuary from river-km 43 to 59, differences between substrates were mainly due to *A. improvisus* with 30.3%. *M. viridis* and *B. ligerica* both contributed with 11.1% to the observed differences. The differences between the groynes and the mussel bed in the outer estuary and the groynes from the inner estuary were mainly caused by *A. improvisus* and *M. edulis*, which contributed to the observed differences with up to 19.6% and 9.1%, respectively. Differences between the sediments of the inner and the outer estuary were mostly due to *M. viridis* which contributed with 16.3% to the differences between the clusters.

3.7. *M. edulis* filtration rate

M. edulis occurred on the groynes from river-km 78 to 90. The average abundance of *M. edulis* in this part of the estuary was 1810 individuals m^{-2}, and the total length of all groynes from river-km 78 to 90 was 9.2 km. This gives for a 3-m wide sublittoral band a

Fig. 4. Result of the cluster analysis (average linkage) using Bray–Curtis dissimilarity values with the samples from groynes and sediments. Numbers in parentheses indicate the river-km. Significantly different clusters (A–E) were identified using the SIMPROF procedure. For the species contributing most to the differences between clusters (SIMPER analysis) see Table 3.

total area of 0.2 km^2 supporting 2.2×10^8 individuals of *M. edulis*. Using the filtration rates from the literature, the total volume of water filtered by all mussels in the considered stretch estimates between 91.6 and 183.3 $m^3 \ s^{-1}$. This corresponds to 28—56% of the mean annual discharge of the River Weser. These estimates are based only on the sublittoral abundance of *M. edulis* from our study taking into account only values at depths of 2—3 m below LAT. Much higher mussel abundances are usually present close to the surface (Krone et al., 2013), so that our values are conservative, and much higher values are to be expected when the entire mussel population is taken into account.

4. Discussion

The omnipresence of groynes and other artificial structures and habitats in estuaries has not only dramatically changed their morphology and contributed to the loss of natural habitats (Browne and Chapman, 2011; Perkol-Finkel et al., 2012), but has also created many new habitats for benthic and pelagic (Krone et al., 2013; Harasti et al., 2010) species. Previous experimental studies have investigated the invasibility of the artificial materials by non-indigenous invertebrates (Dafforn et al., 2012). But also the acceptance of artificial hard substrate as habitats for threatened and endangered species has been documented (García-Gómez et al., 2010; Perkol-Finkel et al., 2012). Likewise, the influence of such substrates on the surrounding sediment has been reported (Krone et al., 2013), and it has been shown that artificial structures are usually associated with high benthic diversity (Bustamante et al., 2007). In the present study we investigated the benthic fauna on both groynes and in the sediment in a typical Wadden Sea estuary, where natural geologically derived hard substrate is absent. We showed that groynes support diverse and abundant benthic communities with more species in higher numbers than occurred in the sediment. However, NIS as well as threatened and endangered species did not show significantly higher abundance, biomass, and numbers of species on the groynes, although some NIS were exclusively present on the groynes. In addition, especially suspension feeders like *M. edulis* were highly associated with the artificial hard-substrate. So we estimated the total filtration rate of all *M. edulis* individuals in a 12 km stretch to reach 56% of the average annual river discharge into the estuary.

The artificial hard-substrate of the groynes had the highest values of total abundance, biomass, and number of species. We found 35 taxa on the artificial hard substrates and only 12 in the sediment samples. This pattern coincides with many other studies on artificial substrates (e.g. Davis et al., 1982; French and Livesey, 2000; Bustamante et al., 2007). In our study, some species were present on the groynes in high abundances such as *B. ligerica* which is also found in other Wadden Sea estuaries (cf. Wetzel et al., 2012), or exclusively like *P. hirtellus*, *E. sinensis*, *Monocorophium insidiosum*, *Parapleustes assimilis*, and *Stenothoe marina*. These species have not been documented in earlier studies of the Weser estuary focussing on sublittoral sediments (see Dittmer, 1981; Gosselck et al., 1993). This indicates that a benthic community has established on the groynes that is very different from the natural sediment community of this Wadden Sea estuary.

Though we did not find any significant difference between substrates in terms of the number, abundance, and biomass of threatened species, several of these species like *B. ligerica* and *A. lacustre* populated the artificial hard-substrates in high abundances. This indicates the potential of such substrates to provide a suitable habitat for threatened and endangered species (Perkol-Finkel et al., 2012). But why are these species considered endangered when they populate artificial habitats in high abundances? The crux of the matter is that natural, geologically derived hard-

Table 3
Results of the SIMPER analysis showing the contribution (%) of the species responsible for the differences observed between the clusters identified in the SIMPROF procedure. Only the topmost six values that contribute to the differences between the clusters are displayed. The highest contribution of a species to the differences between two groups is highlighted in bold.

Species	A–B	C–B	D–A	D–B	D–C	D–E	E–A	E–B	E–C
Bivalvia									
Mya arenaria		5.0							
Mytilus edulis	**9.2**		9.1				5.9		
Oligochaeta					4.7				
Polychaeta									
Eteone longa		6.2							
Alitta succinea	4.3					5.0		6.5	7.4
Lepidonotus squamatus					2.9				
Nephtys hombergii	4.7	8.1		6.4				3.9	
Boccardiella ligerica						10.6	8.4	10.6	11.1
Marenzelleria viridis		**16.3**	7.1	5.4	11.0		5.3		5.6
Heteromastus filiformis	5.7	10.0		7.9				4.8	
Scoloplos armiger		7.3		5.9					
Maxillopoda									
Balanus crenatus	6.1		6.1				4.6		
Amphibalanus improvisus			**14.9**	**24.4**	**30.3**	**11.7**	**19.6**	**26.8**	**30.3**
Carcinus maenas		5.0							
Eriocheir sinensis						3.3			3.8
Gammarus zaddachi						3.2			
Apocorophium lacustre				5.6	5.4	7.5	8.7	11.0	11.6
Corophium multisetosum					4.1				
Gammarus salinus	6.5		6.4						

substrates are absent in the Wadden Sea, so that these hard-substrate dwelling species occur automatically in much lower abundances than soft-substrate dwellers that have practically the entire Wadden Sea as their potential habitat. Indeed, many species that are considered endangered according to Petersen et al. (1996) are hard-substrate dependent species.

The strong presence of threatened and endangered species on the groynes shows that not only natural habitats need to be considered when threatened-species lists are established. The importance of artificial hard substrates for many estuarine species, including possibly threatened-species, has been underrated so far. Especially under the aspect of the WFD and the MSFD, artificial hard substrates need to be included when the EQS of the estuarine water bodies is estimated. So far, only soft-substrate habitats have been included in the development and application of benthic-relevant WFD indicators for estuaries (e.g. Borja et al., 2000; Rosenberg et al., 2004; Dauvin and Rullet, 2007). Hard-substrate depending benthos, however, has been largely neglected, though some attempts have been made to apply existing soft-bottom indicators to hard-substrate environments (Kalkan et al., 2007) or to develop specific indicators for this requirement (Orlando-Bonaca et al., 2012).

Artificial hard-substrates do improve the situation for selected species by providing them with a habitable space, but do we elevate the ecological value of estuaries by adding artificial structures? Is it not rather so that the addition of artificial habitats contributes to the loss of the natural sediment habitats? The primordial Wadden Sea was free of rock (Reise, 2005) so that any artificial structure like breakwaters and groynes conflicts with this natural pristine status. Today, along the entire Wadden-Sea coast, from south Denmark, via Germany to The Netherlands, an area of approximately 0.05–0.1% (2–4 km^2) is covered with artificial hard-substrate (Reise, 2005). Nevertheless, the total loss of sediment areas and habitats through all artificial structures is still small in comparison with the omnipresence of the sediment environment. The total sublittoral area of the Wadden Sea comprises an area of about 4000 km^2 (Reise, 2005), so that the loss of natural habitat as a consequence of built-in artificial substrates is not much of an issue in Wadden Sea estuaries.

Many natural habitats that were once present in the Wadden Sea and their estuaries have disappeared. Subtidal *Zostera marina*

beds have been whipped out in the 1930s through a wasting disease, while overexploitation of natural oyster beds had led to their extinction in the 1950s (Reise et al., 1989). At the same time, reefs built by the polychaete *Sabellaria spinulosa* were systematically destroyed with anchor chains because these reefs interfered with bottom-trawling fishery (Reise and Schubert, 1987). With the loss of these habitats, their associated communities have disappeared as well (cf. Reise et al., 1989) resulting in the decline of sessile species abundances (Buhs and Reise, 1997; Reise et al., 1989; Reise and Buhs, 1999; Lotze, 2005) and reducing the former filtering and retention capacity of the estuaries (cf. Reise, 2005). Today's artificial substrates (e.g. groynes) may provide new habitats and refuges for some of these hard-substrate dependent invertebrate species. Nevertheless, such a putative re-colonization of former biotic reef species may have resulted in reduced genetic diversity in many of today's artificial hard-substrate species (Fauvelot et al., 2009, 2012). Reduced genetic diversity might decrease population stability, because certain genotypes are less fit (Alberte et al., 1994) which could result in reduced size or less reproduction success of species dwelling on artificial hard-substrate.

NIS did not occur overproportionally on the artificial hard substrate. In our study we found no significant difference between substrates; three species were present (*A. improvisus*, *E. sinensis*, and *M. viridis*). These species have been part of the indigenous species communities at the German North Sea coast and the estuaries since 1858, 1912, and 1996, respectively (Gollasch and Nehring, 2006). Our results are within the range found in other studies. For example, Tyrrell and Byers (2007) observed the settlement of three macrobenthic NIS on artificial substrates in an embayment at the coast of Maine, USA, and Pister (2009) found two macrobenthic NIS on coastal defence structures made of rip-rap in southern California, USA. Wasson et al. (2005), however, mentioned 12 macrobenthic NIS on artificial hard substrates in the Elkhorn Slough estuary, California of which seven species were bryozoans. Nevertheless, other studies have shown high potential of artificial hard substrates to be invaded by alien species (Dafforn et al., 2012; Ruiz et al., 2009; Glasby et al., 2007), and thus more NIS are to be expected on such substrates in the future.

The most prominent feeding guild on the artificial hard-substrates was that of the suspension-feeders (cf. Fig. 3), mainly *A. improvisus* and *M. edulis*, with abundances ranging from 43 to 6730 individuals m^{-2} which corresponds to relative abundances of 62.6 and 97.7%, respectively. In contrast, on soft substrates suspension-feeders reached a maximum abundance of 2 individuals m^{-2} corresponding to 9.3% of all sediment-dwelling individuals. The total filtration rate of *M. edulis* on the artificial hard-substrates alone in a 12 km river stretch has been estimated by us to reach almost 56% of the mean annual estuarine freshwater discharge. Accordingly, the filtration by *M. edulis* is expected to influence the water clearance at least on a local scale, and filtration by balanid species (*A. improvisus* and *B. crenatus*) will add to this influence on the estuarine water column. This high dominance of suspension-feeders associated with artificial hard-substrates must have an important effect not only on the benthic communities of the particular substrate but on the entire ecosystem.

In the water column, the hard-substrate dependent suspension-feeders may decrease planktonic algae (Riemann et al., 1988; Olsson et al., 1992; Granéli et al., 1993; Prins et al., 1995; Dame, 1996), and thus indirectly affect zooplankton through food competition. However, suspension feeders are also known to capture zooplankton directly, like copepod nauplii, in high rates (e.g. Davenport et al., 2000), and thus to change the pelagic food-web structure (Prins and Escaravage, 2005). Dreissenid mussels have been shown to significantly remove suspended particulate matter from the water column, thus improving water clarity in lakes and rivers (Higgins and Vander Zanden, 2010). Furthermore, mussels are known to reduce also total nitrogen in the water column of estuaries and could be effective in recycling nutrients from sea to land (Lindahl et al., 2005).

For the sediments in the vicinity of groynes, bivalve suspension-feeders on the groynes act as a link between the pelagic and the benthic processes (cf. Coen et al., 2007; Hatcher et al., 1994; Newell et al., 2005) by consuming seston from the water column and depositing feces and pseudofeces on the sediment surface, thus causing an organic enrichment of the surrounding sediments (Newell et al., 2005; Krone et al., 2013) especially by increasing the total dissolved nitrogen (Hatcher et al., 1994). These changes in sediment chemistry can affect benthic communities by increasing or decreasing individual species abundances (Dauer et al., 2000) or by changing entire species compositions (Kaspar et al., 1985). Severe eutrophication may facilitate hypoxic or even anoxic conditions, which would favour changes in the species composition of benthic communities even more (cf. Diaz and Rosenberg, 2001; Wetzel et al., 2001). Species with high tolerance to oxygen deficiency and to sulphide are favoured (e.g. Wetzel et al., 2002), while more intolerant species are disadvantaged or, when such conditions are not permanent, have to rely on their potential to recover (e.g. Dittmann et al., 1999). The presence of bivalves on the artificial substrates can alter the sediment properties on the surrounding sea bottom or increase the benthic primary production (Ulanowicz and Tuttl, 1992). Mussel-shell litter from deceased animals may serve as basis for attachment that is required by many epifaunal species such as *A. improvisus* and *M. edulis* (Kaspar et al., 1985; Krone et al., 2013). Comminution of shells will also change the sediment from a quartz-dominated to a more shell-dominated substrate (Krone et al., 2013), a change that has also a high potential to affect the surrounding infaunal species composition and sediment characteristics. In fact, artificial reef structures are known to influence the natural communities in their vicinity, such as benthic soft-bottom assemblages (Ambrose and Anderson, 1990; Krone et al., 2013).

The loss of many primordial estuarine habitats such as mussel beds and seagrass beds has impaired important ecosystem services and benefits (Coen et al., 2007; Barbier et al., 2011). Many of these services, such as water purification by filter feeders and seagrass beds, or the availability of nursery habitats provided by biogenic reefs, have been severely reduced or even eliminated over the last centuries (cf. Reise, 2005). These habitats with their high structural complexity are essential in protecting juvenile fish and many invertebrate species from predation (cf. Barbier et al., 2011). Though groynes and jetties represent artificial substrates, their structure is highly complex on a macro-scale (>10 cm) and provides a combination of hard substrate, crevices, pits, and rock pools which provide refuges for many species (Bracewell et al., 2012; Cartwright and Williams, 2012). Artificial reefs, for example, can facilitate and enhance marine communities in coastal and deep-sea environments and provide benefit for ecosystem services in sediment dominated environments (Macreadie et al., 2011). Likewise, groynes and breakwaters provide habitable spaces which many invertebrates and fish can utilize (Bastrop et al., 1997; Burt et al., 2013; Ricciardi and Bourget, 1999). We would not go as far as to claim that these artificial structures have compensated for the loss of habitats, but to a certain, and not yet determined degree, they provide services that go beyond their original purpose as erosion-control structures.

The findings of this study demonstrate that artificial hard-substrates in form of groynes constitute biologically diverse habitats in a sediment dominated Wadden Sea estuary. Groynes support a benthic fauna that differs in many regards significantly from the sediment fauna. In particular suspension-feeding species occur in much higher abundances on groynes and may alter the local food web and affect ecosystem functions and services, such as seston filtration and benthic-pelagic coupling as well. Consequently, artificial substrates should be considered more often in conservation planning (incl. surveys to identify threatened and endangered species), and their role for the ecological quality status according to the European Water Framework Directive, the Habitats Directive, and the Marine Strategy Framework Directive should be taken into account in the future.

Acknowledgements

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