

# The body-size structure of macrobenthos changes predictably along gradients of hydrodynamic stress and organic enrichment

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**Abstract** Body size is related to an extensive number of species traits and ecological processes and has therefore been suggested as an effective metric to assess community changes and ecosystem's state. However, the applicability of body size as an ecological indicator in benthic environments has been hindered by the poor knowledge of the factors influencing the size spectra of organisms. By applying biological trait analysis (BTA) and generalized linear models to a species dataset collected in the German Wadden Sea (53°41'14" N, 7°14'19" E) between 1999 and 2012, we show that the size structure of the macrobenthic community changes predictably along environmental gradients. Specifically, body size increases with increasing current-induced shear stress and sediment organic matter content. In addition, the presence of oyster–mussel reefs in one of the sampling stations enhanced the survival of species belonging to

the smallest size categories in habitats with high hydrodynamic energy. This was probably due to the local sheltering effects, which together with biodeposition also increased organic matter in the sediment, likely favoring large deposit feeders as well. Our results suggest that body size can be a useful trait for estimating effects of anthropogenic stressors, such as organic enrichment or alteration of hydrodynamic regime and could therefore be effectively included in current monitoring programs of intertidal macrobenthic communities.

## Introduction

Body size is a key trait and one of the most studied attributes of organisms in biology and ecology. Body size affects biological processes at all levels of organization, from cell metabolism to population dynamics (e.g., Gould 1966; Calder 1984; Schmidt-Nielsen 1984; West et al. 1997; Brown et al. 2004), eventually influencing speciation and extinction rates of organisms (Etienne et al. 2012). Among

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aquatic ecologists, the interest in body size started in the 1960s with the investigation of the body-size structure of planktonic communities (Hrbacek et al. 1961; Brooks and Dodson 1965) and later on the size structure of benthic communities and the factors controlling it (e.g., Schwinghamer 1981; Warwick 1984; Strayer 1991; MacDonald et al. 2012). The promising results coming from this work contributed to a conspicuous line of research focusing on causes and consequences of body size as a master trait in biological communities (Peters 1983; Litchman and Klausmeier 2008).

One of the main reasons of interest in body size lies in its potential application as an ecological descriptor of community properties and state. First of all, body size is related to many life-history traits of species and ecological processes, for example, metabolic (Kleibert 1932; Zeuthen 1953; Gillooly et al. 2001) and reproductive rate (Brown et al. 1993), longevity (Schmidt-Nielsen 1984; Marquet et al. 2005) and interaction strength (Emmerson and Raffaelli 2004). Hence, body-size spectra can provide useful information about the community energetics and ecosystem functioning (e.g., Borgmann 1987; Woodward et al. 2005). Second, size-based approaches are a form of taxon-free classification of ecological assemblages (Damuth 1992) that allow comparison of communities with different species composition (Sprules and Munawar 1986; Mouillot et al. 2006). Especially in large-scale monitoring programs, body size could be a valuable trait to assess ecosystem health across different regions and over time.

While for pelagic communities size-based approaches have found wide application (e.g., Mills et al. 1987; Reizopoulou and Nicolaidou 2007), their applicability in benthic ecosystems has been lagging behind. This is partly due to inconsistent results from previous studies and a poor knowledge of the factors regulating the size structure of benthic communities (Edgar et al. 1994; Robson et al. 2005). Benthic environments display much higher complexity and heterogeneity than pelagic ones and body-size relationships may underlie a large variety of mechanisms (Allen et al. 2006; Yamanaka et al. 2012). In planktonic communities, vertebrate predation is a major determinant of body-size spectra, as fish predators are strongly size-selective (Brooks and Dodson 1965; Šorf et al. 2014). In benthic environments, however, organisms can find refuge among the fronds of macroalgae or in sediment interstices, and therefore, environmental factors such as habitat architecture and substrate composition strongly affect the size structure of benthic communities (Strayer 1991; Holling 1992; Schmid 2000; Tokeshi and Arakaki 2012). In fact, the availability of shelters of different dimensions influences the size of crabs (Beck 1995), and different morphologies of macroalgae as well as different levels of habitat complexity determine the size spectra of amphipods

(Hacker and Steneck 1990), gastropods (Pennings 1990), epifaunal (Gee and Warwick 1994) and infaunal assemblages (Schmid et al. 2002).

In soft-bottom systems, the body-size structure of benthic organisms has traditionally been attributed to physical constraints determined by the grain size composition of the sediment, i.e., energetic inefficiencies can hinder fauna penetrating through sediments at sizes slightly larger than the sediment pore size (Schwinghamer 1981). However, this idea has long been questioned (Edgar et al. 1994; Bourassa and Morin 1995; Parry et al. 1999; Leaper et al. 2001; Dolbeth et al. 2014), and effects of other sediment properties, such as organic matter content, have been investigated. In the Strait of Georgia, small organisms dominate shallow habitats with coarse sediments and low organic matter input, while large organisms abound in deeper organic-rich sediments (MacDonald et al. 2012). Sediment organic matter was also found to be positively correlated to the lengths of nematodes in the Genoa-Voltri harbor (Losi et al. 2013). In contrast to this focus on sediment properties, only few studies have considered the importance of hydrodynamic conditions in driving body-size patterns of benthic species (McLachlan and Dorvlo 2007; Defeo and McLachlan 2011, 2013). These studies show that body size of macrobenthos decreases from reflective to dissipative beaches, suggesting a positive relationship between hydrodynamic energy and organism body size. Indeed, dragging forces caused by water currents influence several morphological traits of species, from body shape to surface roughness and flexibility (Koehl 1996), and especially in streams and tide-dominated systems such as intertidal flats, they can be crucial for settlement, mobility and acquisition of food by the benthic fauna (Denny and Wethey 2001).

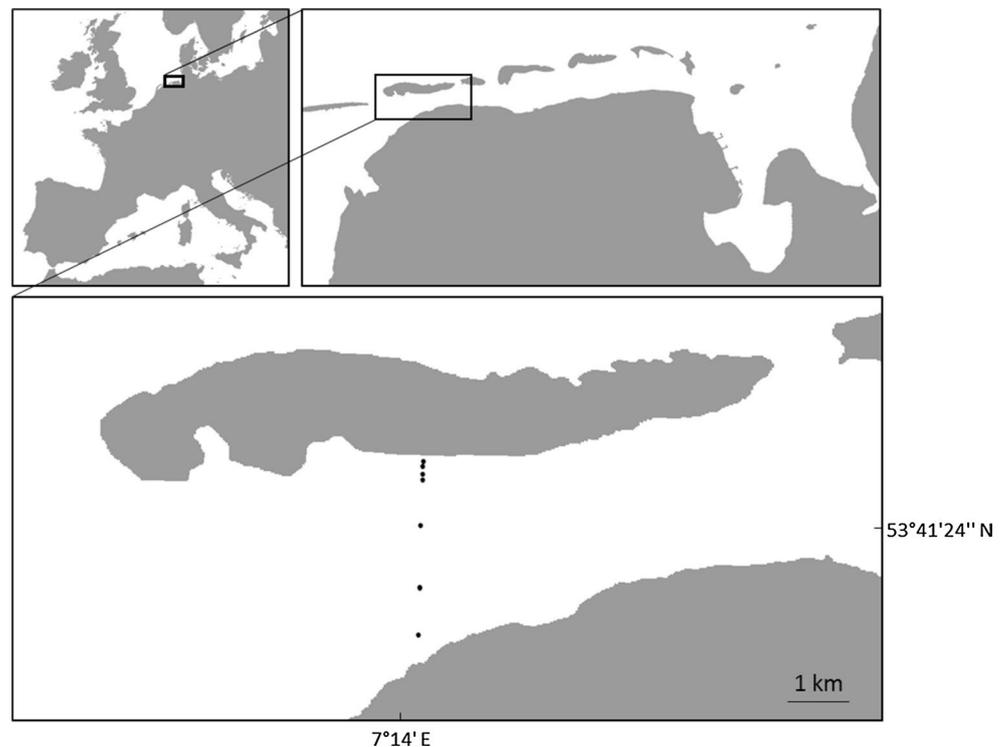
The aim of our study was to determine whether body-size structure of macrobenthos could be used to assess the state of soft-bottom intertidal ecosystems in relation to sediment and hydrodynamic conditions, which are both important environmental drivers on tidal flats that are strongly affected by human influences. To qualify as a good indicator, the body-size structure needs to vary predictably along gradients of abiotic and/or biotic stressors that are directly or indirectly related to ecosystem health. We analyzed a dataset containing species biomass values from 268 samples collected during a 14-year-long monitoring campaign in the German Wadden Sea. To detect community-level effects, the whole macrobenthic community was sampled at eight stations with different environmental conditions and at different distances from the coast. We investigated the relation between body-size structure of the macrobenthos and (1) several sediment parameters and (2) current-induced shear stress, which indicates habitat hydrodynamic energy.

## Materials and methods

### Data

The dataset was provided by the Lower Saxony Water Management, Coastal Defence and Nature Conservation Agency and the National Park “Niedersächsisches Wattenmeer.” Data were collected during multiple monitoring campaigns [German Marine Monitoring Program (BLMP), Trilateral Monitoring and Assessment Program (TMAP), Joint Assessment and Monitoring Program (JAMP)] over 14 years between 1999 and 2012. Samples were taken at eight sampling stations (St. 1–St. 8) in the intertidal (heights above sea level between 0.43 and  $-1.06$  m) along a transect between the island of Norderney and the German mainland ( $53^{\circ}41'14''$  N,  $7^{\circ}14'19''$  E; Fig. 1). St. 1–St. 4 were visited four times a year between 1999 and 2006 and twice a year between 2007 and 2012, with the exception of St. 4, which was not sampled again after 2006. In the other stations, sampling was carried out twice a year, resulting in a total of 268 unique samples, collected at different times of the year (96 samples in April–June, 72 in July–September, 59 in October–November and 41 in January–March). St. 6 and St. 7 are located at the same tidal elevation, 30 m far apart, as they represent the different communities on an oyster-mussel bed and in an area without reef-building bivalves, respectively. For the other stations, the closest distance to each other was about 150 m, while the maximum distance was about 1,000 m.

**Fig. 1** Map of the sampling area. Samples were taken at eight sampling stations along a transect between the island of Norderney and the German mainland



### Macrofauna

For each sampling occasion, ten sampling cylinders (area =  $181.46$  cm<sup>2</sup>, total sampled area =  $0.181$  m<sup>2</sup>) were extracted from the sediment to a depth of 30 cm and sieved over a 1-mm mesh. All organisms were counted and identified (mostly to species level) and ash-free dry weight (AFDW) of biomass of each taxon in each sample was determined by loss on ignition (3 h,  $495$  °C) after drying until constant weight (48 h,  $60$  °C). In total, 2,995,379 individuals belonging to 108 taxa were collected, of which polychaetes, crustaceans and mollusks were dominant, contributing 56, 31 and 21 species, respectively. Biomass of spat, juveniles and adults was measured separately for some of the most common and largest bivalves, i.e., *Cerastoderma edule*, *Crassostrea gigas*, *Ensis directus*, *Macoma balthica*, *Mya arenaria*, *Mytilus edulis*, *Scrobicularia plana*.

### Sediment parameters

At each sampling station, sediment was extracted to a depth of 5 cm with a PVC corer with area of  $181.46$  cm<sup>2</sup>. Percentages of sediment water content, organic matter content (LOI), total organic carbon content (TOC), total carbon content (TC) and silt content (sediment fraction  $<63$  μm) were determined according to the protocols provided by the German Institute for Standardization (DIN). Pore water salinity (psu) and pH were measured in the laboratory with

conductivity and a pH meter (WTW InoLab Cond 730 and WTW pH 3210, Germany) shortly after sampling. Mean oxygenation depth was estimated by measuring with a ruler the depth of the black anoxic sediment of five sampling cylinders extracted from the sediment with the PVC corer.

#### Current-induced shear stress

The bed shear stress is the frictional force exerted on unit area of sea bed by the current flowing over it. It represents the flow-induced force acting on sand grains on the bed and is therefore an important quantity for transport of sediments and particles at the sea bottom (Soulsby 1997). Mean and maximum current-induced shear stress were estimated over a time interval of 6 days based on hydrodynamic model simulations performed with a regional coastal ocean model for the German Bight. In detail, the unstructured grid finite-volume coastal ocean model FVCOM (see e.g., Chen et al. 2003) was used to calculate tide-induced currents within the German Bight with a special focus on the East-Frisian Wadden. As the water column within the area of the East-Frisian islands is vertically well mixed throughout the year (Becker et al. 1992), density-dependent processes can be considered of minor importance with respect to coastal currents and current-related bed shear stress estimations in that area. Therefore, the model was run in a constant-density (barotropic) mode, with a varying horizontal resolution between 200 and 500 m close to the island of Norderney. In the vertical, the model used five terrain-following sigma layers. The model was extensively validated by means of surface elevation data and ADCP current data. Due to the sheltering effect of the East-Frisian islands from wind-generated surface waves of the open North Sea, within the backbarrier area of Norderney, wave-induced bed shear stress components can also be considered of minor importance (Lettmann et al. 2009; Kösters and Winter 2014). Therefore, only the current-induced skin-friction shear stress ( $\tau$ ) was calculated using the current velocity components within the deepest vertical layer by means of the following formula (see e.g., Warner et al. 2008):

$$\tau = \frac{\rho \kappa^2}{\ln^2(z/z_0)} (u^2 + v^2)$$

Here,  $\rho = 1,025 \text{ kg/m}^3$  denotes the constant water density,  $\kappa = 0.41$  von Kármán's constant,  $z$  the height above bed of the mid point of the deepest vertical layer,  $z_0 = 0.2 \text{ mm}$  a constant representative of bottom roughness, and finally,  $u$  and  $v$  the horizontal velocity components above bed. It should be noted that the estimated mean and maximum current-induced shear stress are here used as proxies for ambient hydrodynamic stress in the sampling stations; however,

they do not account for local bottom features, such as oyster-mussel reefs that could affect water flow dynamics.

#### Statistical analysis

To investigate the body-size spectra of the macrobenthic community, we applied biological trait analysis (BTA). BTA is a trait-based approach that is increasingly used to describe the ecological functioning of an assemblage (Bremner et al. 2006). This can be particularly useful when absolute measurements of numerical species attributes are not available. Based on Jones and Frid (2009), we identified seven categories of body size, with the categories “taxa smaller than 5 mm” and “taxa larger than 160 mm” at the two extremes of a size gradient (see Electronic Supplemental Material 1). To account for intraspecific (inter-annual) variability in body size, individual taxa were scored for the extent to which they display the size category using a “fuzzy coding” procedure (Chevenet et al. 1994), which allowed taxa to exhibit size categories to different degrees. Also, when separate biomass values were available for different life stages (see Materials and methods—*Macrofauna*), spat, juveniles and adults of the same species were treated as separate taxa and were therefore assigned to different size categories. Information on taxa body size was obtained from online databases for north European marine invertebrates and published peer-reviewed studies on the Wadden Sea region. Taxa were scored from 0 to 3, with 0 being no affinity and 3 being total affinity to a size category. Fuzzy scores were standardized in such a way that the sum of scores for each taxon summed to 1 (Electronic Supplemental Material 1). For example, the species *Crepidula fornicata* shows 0.17 scores for the size category 5–10 mm, 0.50 scores for the category 20–40 mm and 0.33 scores for the category 40–80 mm, meaning that 17 % of individuals counted (or biomass measured) is assumed to measure between 5 and 10 mm, 50 % between 20 and 40 mm, and 33 % between 40 and 80 mm (Electronic Supplemental Material 1). The number of taxa for which scores were different from zero in each size category was, respectively, 20 for “taxa smaller than 5 mm,” 42 for “taxa between 5 and 10 mm,” 60 for “taxa between 10 and 20 mm,” 63 for “taxa between 20 and 40 mm,” 46 for “taxa between 40 and 80 mm,” 30 for “taxa between 80 and 160 mm” and 11 for “taxa above 160 mm.” Size category scores of each taxon were multiplied by the biomass of the taxon for every sample and subsequently summed across all taxa to provide a sample-by-trait matrix containing a total biomass score for each size category and for each sample (Charvet et al. 1998). This sample-by-trait matrix, containing a total of 268 samples and 8 size categories, was analyzed using principal component analyses (PCA). Gradient lengths were first estimated in a detrended correspondence

analysis (DCA). As the lengths of DCA axes 1 and 2 were both lower than 2, we used PCA, which assumes linear responses of species to environmental gradients (ter Braak and Smilauer 2002). Matrix data were square rooted prior to ordination to reduce skewness.

Correlations between environmental factors were explored by computing a matrix of Spearman's rank correlation coefficients for all possible pairs of covariates. High levels of positive multicollinearity were detected between LOI, TOC, TC, silt and water content, and between mean shear stress, maximum shear stress and distance from the coast.

To explore the relationship between size categories and habitat conditions, we calculated weighted averages of organic matter content (LOI) and mean shear stress for each size category using the formula:

$$\text{Weighted Average}_j = \frac{1}{N} \sum_{i=1}^N (x_i z_{ji})$$

where  $x_i$  is either organic matter content or mean shear stress of sample  $i$ ,  $z_{ji}$  is the biomass score of sample  $i$  for the size category  $j$ , and  $N$  is the total number of samples. Weighted averages therefore indicate environmental conditions at which each category was observed most frequently. To investigate associations between different size categories and environmental conditions, weighted averages for all categories were plotted for organic matter content and mean shear stress. Standard errors of weighted averages were calculated following Cochran (1977), as suggested by Gatz and Smith (1995). LOI and mean shear stress were chosen among the other environmental factors based on biological knowledge and lack of collinearity, which was likely due to different levels of precision in the estimation, i.e., LOI values were measured in the field and therefore better reflected local variability, while mean shear stress values were estimated on larger areas by models that did not account for factors locally modifying the hydrodynamic regime. To investigate the influence of oyster-mussel reefs on the relationship between body-size structure and environmental factors, weighted averages were calculated separately for the full dataset and for a subset not including the station located on oyster-mussel reefs (St. 6).

The relative effect of environmental factors on individual size categories was investigated through generalized linear models on the subset without Station 6 in order to disentangle the effects of abiotic conditions from those mediated by oyster-mussel reefs. Collinearity among covariates was identified by calculating the variance inflation factor (VIF; Montgomery and Peck 1992) for each predictor. Covariates were dropped sequentially until all VIFs were smaller than 2 (Zuur et al. 2010). Only three variables were retained in the analysis: mean shear stress, organic matter (LOI) and

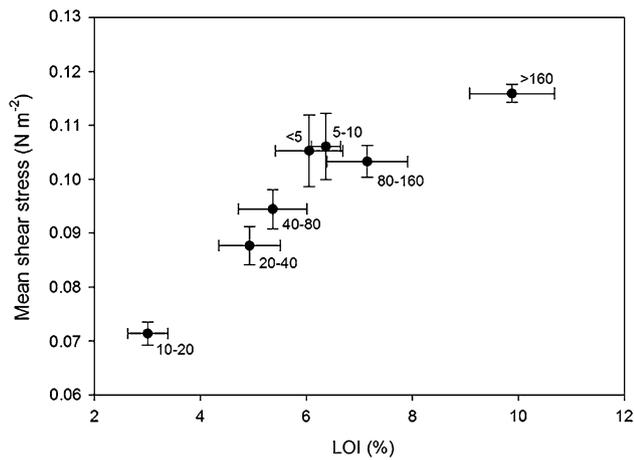
oxidation depth. A negative binomial error distribution with log-link function was selected among other distributions based on the lowest AIC. Significant covariate effects were assessed through a stepwise backward elimination method, where nested models were compared through a likelihood ratio test (LRT). Model validation was performed by plotting residuals versus fitted values and observed versus theoretical quantiles (QQ-plots). Due to the large distance between the sampling stations and the long intervals between sampling occasions compared with the rather short generation times of most benthic invertebrates, data were considered as independent.

Wilcoxon rank sum test was used to test significant differences in organic matter content and ambient mean shear stress between Station 6 (on the oyster-mussel reefs) and the other stations. Multivariate analyses were performed in Canoco for Windows version 4.55 (ter Braak and Smilauer 2002). All the other statistical calculations were carried out in R (CRAN, R: A language and environment for statistical computing, 2010. R Foundation for Statistical computing, Vienna, Austria).

## Results

Species body size increased with increasing sediment organic matter content and hydrodynamic stress (Fig. 2). Averages of organic matter and mean shear stress weighted by the biomass scores of each size category sorted in such a way that the higher the organic matter content and hydrodynamic stress, the larger the species inhabiting the substrate. The only exception to this pattern was given by the very small species (size <5 mm and between 5 and 10 mm), which occurred predominately in habitats with relatively high ambient shear stress and sediment organic matter (Fig. 2). Species that mainly contributed to the weighted averages for largest organisms (size between 80 and 160 mm, and >160 mm) were the bivalves, *Crassostrea gigas* and *Mytilus edulis*, and the polychaetes, *Hediste diversicolor* and *Heteromastus filiformis*. For the smallest species (size <5 mm and between 5 and 10 mm), the main contribution came from the barnacles, *Elminius modestus* and *Semibalanus balanoides*, the gastropod, *Peringia ulvae*, and spat of the bivalve, *Cerastoderma edule*. These species are commonly found in oyster-mussel bed communities and were indeed very abundant in the station located on oyster-mussel reefs (St. 6), suggesting facilitative effects of reef-building bivalves on small-sized species.

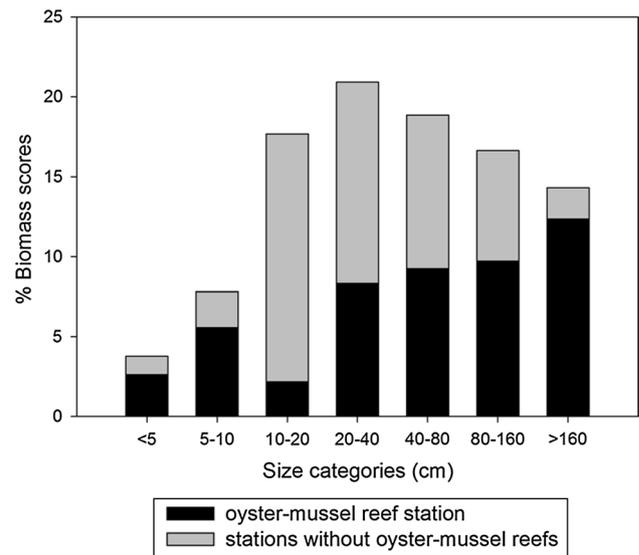
Body-size structure of the macrobenthic community was strongly affected by the presence of mussel-oyster reefs. In the oyster-mussel bed station (St. 6), the percentage of biomass scores of very small and very large species was higher than in the other stations, with a maximum



**Fig. 2** Weighted averages of sediment organic matter content and mean current-induced shear stress for each size category calculated on the full dataset

peak for species larger than 160 mm (Fig. 3). When Station 6 was excluded from the dataset, the more frequent size categories were those of intermediate size, i.e., 10–20 mm and 20–40 mm (Fig. 3). The first two principal components (PC1 and PC2) explained 91 % of the total variance in the biomass scores of size categories, with PC1 and PC2 explaining 82 and 9 % of the total variance, respectively. Both PC1 and PC2 were well correlated to the presence of mussel-oyster reefs, sediment organic matter (LOI) and silt content (Table 1), and PC2 was also correlated with mean shear stress, distance from the coast and total carbon (TC).

Size categories still sorted along gradients of organic matter and hydrodynamic stress when excluding samples from Station 6 (Fig. 4). Without the influence of bivalve reefs, smallest species (size <5 mm and between 5 and 10 mm) were more often found in relatively low-energy habitats. Size generally increased with increasing hydrodynamic stress and organic matter, although very small organisms (size between 5 and 10 mm) and very large ones (size >160 mm) showed deviations from this pattern. However, these size categories had very low biomass scores compared with the others when excluding values from the oyster-mussel reefs station (Fig. 3), which decreased the precision on the estimates. Abiotic ranges of weighted averages shortened, as organic matter and ambient mean shear stress were 72 and 24 % lower, respectively, in stations without oyster-mussel reefs compared with Station 6 (Wilcoxon rank sum test,  $P < 0.001$  for both factors). As a consequence, the pattern looks compressed and standard errors of neighboring values tend to overlap. This is also due to the fuzzy coding technique increasing correlations between biomass of adjacent size categories. Yet, the pattern still suggests that hydrodynamic stress and organic



**Fig. 3** Percentage of biomass scores for each size category in stations without oyster-mussel reefs (gray) and in the oyster-mussel reef station (black)

matter are important structuring factors for the size spectra of the intertidal macrobenthic community.

Without oyster-mussel reefs, hydrodynamic stress negatively affected the biomass of small to intermediate-size species, while sediment organic matter had a consistent positive effect on biomass across most size categories (Table 2, Electronic Supplemental Material 2). Percentage of explained deviance of generalized linear models was high (between 31 and 49) for most size categories, showing lower values for the categories at the extreme of the size range (Table 2). Current-induced mean shear stress had a significant negative impact on the size categories going from 5–10 mm to 40–80 mm, with strongest effects on species between 10 and 20 mm (Table 2). Organic matter content explained part of the variation of all but one size category, namely species between 10 and 20 mm, showing the strongest influence on species between 5 and 10 mm and species larger than 160 mm (Table 2). Negative effects of oxidation depth were evident for nearly all size categories, with limited variability in the regression coefficients (Table 2).

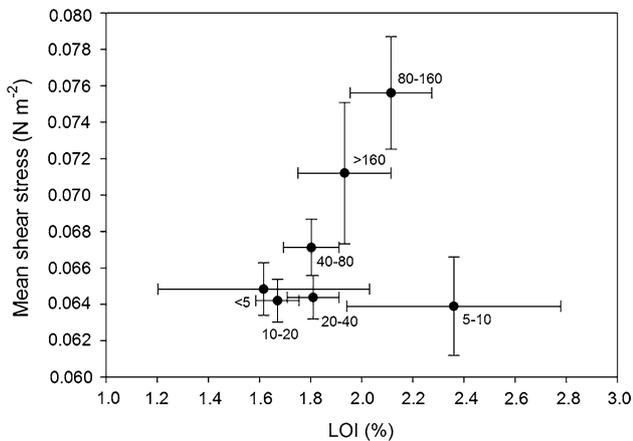
## Discussion

We show that the size distribution of an intertidal community is strongly related to two important environmental factors on tidal flats: sediment organic matter content and hydrodynamic energy. Sediment organic matter is directly related to organic enrichment, and elevated levels are often detected in connection with anthropogenic

**Table 1** Correlations among environmental factors and ordination axes

Environmental factors	PC1	PC2
sediment water content	0.20	0.21
organic matter (LOI)	0.43	0.62
total organic carbon (TOC)	0.25	0.37
total carbon (TC)	0.32	0.46
silt (<63 μm)	0.37	0.57
pH	0	0.08
oxygenation depth	−0.36	−0.22
mean shear stress	0.09	0.48
maximum shear stress	−0.36	−0.22
distance from the coast	0.03	0.43
oyster-mussel bed presence	0.77	0.64

Values are Pearson’s product–moment correlation coefficients



**Fig. 4** Weighted averages of sediment organic matter content and mean current-induced shear stress for each size category after excluding the station located on oyster-mussel reefs

pollution (Airoldi and Beck 2007). Hydrodynamic conditions are affected by common human disturbances in soft-bottom ecosystems, such as damming, diking and dredging

(Eriksson et al. 2010). Thus, the body-size structure of the macrobenthic community can serve as an ecological indicator to directly assess and monitor stress related to human activities on intertidal flats. In addition, we found that an oyster-mussel reef had a strong influence on the size distribution of macrozoobenthos, likely by ameliorating hydrodynamic stress and increasing sediment organic matter content. This demonstrates the importance of ecosystem engineers for habitat conditions and community structure on tidal flats.

We are the first to show that the size of macrobenthic organisms gradually decreases with decreasing hydrodynamic stress. Although there are hints from previous studies of a positive relationship between hydrodynamic energy and the size of macrobenthos (McLachlan and Dorvlo 2007; Defeo and McLachlan 2011, 2013), such relationship had rarely been formally proved. Hydrodynamic processes have a strong influence on benthic recruitment, often causing resuspension of larvae and sediment particles from the substrate (Eckman 1983; Armonies and Hellwig-Armonies 1992; Abelson and Denny 1997; Bouma et al. 2001). Persistence of small organisms may therefore be hampered by the dragging forces of water currents in high-energy environment. Consistently, we found that the very small species (size <5 mm and between 5 and 10 mm) were mainly observed in habitats with low hydrodynamic energy when excluding samples from station 6, and that shear stress had negative effects on small to intermediate-size species. However, the presence of an oyster-mussel reef allowed the persistence of small organisms, such as *Elminius modestus*, *Semibalanus balanoides*, *Peringia ulvae* and *Cerastoderma edule* spat, in habitats where ambient shear stress was relatively high, thus causing an apparent deviation from the described relationship between body size and hydrodynamic energy. This is caused by shear stress values being estimated from spatially explicit models that do not show local variation caused by small-scale seabed structures, such as oyster or mussel reefs. Our results are in agreement with previous evidence of enhanced settlement of

**Table 2** Coefficients of generalized linear models examining effects of environmental factors on the biomass scores of each size category

	<5 mm		5–10 mm		10–20 mm		20–40 mm		40–80 mm		80–160 mm		>160 mm	
	Coeff.	P	Coeff.	P	Coeff.	P	Coeff.	P	Coeff.	P	Coeff.	P	Coeff.	P
Mean shear stress			−10.93	**	−15.84	***	−14.72	***	−8.58	***				
LOI	0.40	***	0.64	***			0.30	***	0.25	***	0.27	***	0.51	***
Oxidation depth	−0.31	**	−0.27	***			−0.20	***	−0.25	***	−0.23	***	−0.20	**
% Deviance	13		31		49		48		38		12		18	

The percentage of explained deviance by the model is provided. Models assume a negative binomial error distribution with log-link function. Only significant coefficients are shown. Significance level ( $\alpha$ ) was set at 0.05 of probability

\*\*\*  $P < 0.001$ ; \*\*  $P < 0.01$ ; \*  $P < 0.05$

macrozoobenthos and *C. edule* recruits in the lee of mussel or oyster reefs due to declining hydrodynamic energy (Widdows and Brinsley 2002; Commito et al. 2005; Donadi et al. 2013, 2014). Body-size spectra could therefore provide information about the habitat hydrodynamic regime and the factors that locally modify it, such as natural ecosystem engineers (i.e., bivalve reefs and seagrass beds) or anthropogenic stressors (i.e., dredging, coastal engineering).

Our analysis showed that body size increased with increasing sediment organic matter content. An exception to this pattern was represented by the very small species, whose biomass was strongly affected by the presence of the oyster-mussel bed. Recent studies demonstrate that such positive relationship between body size and sediment organic content may be a recurrent pattern among macro- and meiobenthic organisms (MacDonald et al. 2012; Losi et al. 2013; but see Raffaelli et al. 2000). According to Thiel's hypothesis (1975), we speculate that this might be partly due to food availability (i.e., organic matter) facilitating the dominance of large-sized species. Indeed, some of the large species contributing to the observed pattern were *Hediste diversicolor* and *Heteromastus filiformis*, which are primarily deposit feeders. However, among the strongest contributors, we also found suspension feeders, such as *Crassostrea gigas* and *Mytilus edulis*. These reef-forming bivalves alter the sedimentation regime through biodeposition and hydrodynamic stress alleviation (Graf and Rosenberg 1997; Donadi et al. 2013) and were likely responsible for high local levels of organic matter in the sediment. The sorting of body size along a gradient of sediment organic matter may therefore be caused by organic content being either a source of food for large deposit feeders or a product of ecosystem engineering of large reef-forming bivalves. Alternatively, the pattern may be driven by other environmental factors which covary with organic matter, for example, grain size. Coarse sediments, besides containing little food for deposit feeders, are often unstable and large sedentary burrowers may be limited on their ability to maintain an optimal burrow position (Bromley 1990), while small organisms may be facilitated by the large interstitial spaces in sandy substrates (Wigley and McIntyre 1964). Also, small species may become less competitive in muddier sediments due to increased predation by subsurface deposit feeders (MacDonald et al. 2012). Finally, it may also be that traits other than body size contributed to the observed patterns. However, the high number of taxa included in each size category (see [Materials and methods](#)), our large sample size, together with results from additional analyses on the same dataset considering nine different traits (unpublished results), strongly support our conclusions. Nonetheless, there are many traits that covary with body size (e.g., living depth), and we cannot exclude that

these played a key role in mediating the response of taxa to habitat conditions. Further studies and future experiments will contribute to shed light on the relationships between macrobenthos traits and environment, and the underlying mechanisms.

Ecosystem engineers such as bivalve reefs had a strong effect on the size structure of the macrobenthic community. The presence of an oyster-mussel bed in Station 6 enhanced the biomass of species at the extremes of the size gradient, possibly allowing the survival of small organisms in high-energy environments (Commito et al. 2005; Donadi et al. 2013), while facilitating large deposit feeders by increasing sediment organic matter through biodeposition (Kröncke 1996). By changing environmental conditions, ecosystem engineers alter the variety of ecological niches available to other species (Jones et al. 1994) and can therefore enhance regional species richness (e.g., Wright et al. 2002), but also change the functional trait composition (e.g., Volkenborn and Reise 2007—this study). This may entail important consequences for community properties and ecosystem functioning. Body size is strongly related to many life-history traits and processes affecting multiple levels of biological organization (e.g., West et al. 1997; De Roos et al. 2003; Brown et al. 2004), and hence, changes in body-size spectra will likely have profound effects in the functions, energy fluxes and dynamics of the whole community, eventually affecting ecological stability and resilience to disturbance (Emmerson and Raffaelli 2004; Solan et al. 2004; Woodward et al. 2005). Therefore, by changing the size spectra of the surrounding communities, ecosystem engineering could deeply affect their functioning and dynamics.

Body size has been suggested as an effective alternative to taxonomy-based metrics to assess community changes and to aid predictions on the effects of anthropogenic disturbances on ecosystem properties (Mouillot et al. 2006; Borja et al. 2011; Pinna et al. 2014). Despite some critics (Robson et al. 2005), body size has been suggested as a suitable descriptor of lagoon ecosystem health (Reizopoulou and Nicolaidou 2007; Basset et al. 2012; Pinna et al. 2013) and is already included as an optional parameter in the guidelines for monitoring transitional water ecosystems (Common Implementation Strategy for the WFD, 2003) and in the Marine Strategy Framework Directive for the environmental status assessment of European marine and coastal waters (European Commission 2010/477/EU, 2010). Our analysis shows that the size structure of a macrobenthic intertidal community is affected by sediment organic matter and hydrodynamic stress and could therefore serve as a practical alternative for estimating disturbance impacts such as organic enrichment or alteration of hydrodynamic regime. Although the observed patterns and the

underlying mechanisms need to be validated by further investigation and local reference conditions for size-based indicators remain to be set, we believe that our results contribute toward the applicability of body size as a useful indicator in monitoring programs.

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**Conflict of interest** Serena Donadi, Britas Klemens Eriksson, Karsten Alexander Lettmann, Dorothee Hodapp, Jörg-Olaf Wolff and Helmut Hillebrand declare that they have no conflict of interest. All institutional and national guidelines for the care and use of laboratory animals were followed.

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