LIMNOLOGY and OCEANOGRAPHY

Sediment properties, biota, and local habitat structure explain variation in the erodibility of coastal sediments

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Abstract

Sediment resuspension is a frequent phenomenon in coastal areas and a key driver for many ecosystem functions. Sediment resuspension is often linked to biological and anthropogenic activities, which in combination with hydrodynamic forcing initiate sediment erosion and resuspension, if the erosion threshold (τ_c) is exceeded. Despite its importance to ecosystem functions very few studies have provided measurements on natural assemblages for subtidal sediments. The aim of this study was to determinate key environmental variables regulating sediment resuspension potential across a sedimentary gradient in a subtidal coastal environment. In order to explore this, we sampled 16 sites encompassing a wide variety in environmental variables (e.g., grain size distribution, macrofaunal communities, vegetation) in the Gulf of Finland, Baltic Sea. A core-based erosion device (EROMES) was used to determine sediment resuspension potential measures of erosion threshold, erosion rate (ER), and erosion constant (m_e). Based on abiotic and biotic properties sampled, sediments diverged into two distinct groups; cohesive ("muddy") and noncohesive ("sandy") sediments. Results showed that abiotic sediment properties explained 38–53% and 15–36% of the total variation in resuspension potential measures in "muddy" and "sandy" sediments, respectively. In cumulative models, biota accounted for 12–26% and 6–24% to the total variation in "muddy" and "sandy" sediments, respectively. Sediment erodibility and resuspension potential of natural sediments is highly variable from local habitats to a larger seascape scale. Our results underline the importance of biota to resuspension potential measures in spatially variable environments.

Coastal areas maintain valuable ecosystem services and functions for human and marine life. These dynamic environments are highly productive and diverse, and they play a central role in the transfer of matter, energy and organisms (Barbier et al. 2011; Levin et al. 2001). Sediment resuspension is a frequent phenomenon in coastal areas and a key driver for many ecosystem functions (Danielsson et al. 2007). For example, pollutant dispersal, seafloor colonization dynamics, and biogeochemical cycles are all influenced by sediment resuspension (Warrick 2013). In addition, sediment

resuspension elevates water turbidity and changes oxygen concentrations impacting both benthic and pelagic ecology (Alongi and McKinnon 2005; Bilotta and Brazier 2008; Almroth et al. 2009). Sediment resuspension in shallow coastal areas is generally regulated by wind-waves and currents that generate shear stress on the sediment surface (e.g., Sanford and Maa 2001; Ziervogel and Bohling 2003; Danielsson et al. 2007; Valanko et al. 2010; Green and Coco 2014), but internal waves, seiches, biological activity, and anthropogenic actions can also cause sediment resuspension (e.g., Weyhenmeyer 1998; Duplisea et al. 2001). Erosion and resuspension in cohesive "muddy" sediments is often a result of bed failure (Hayter and Mehta 1986) whereas in non-cohesive "sandy" sediments, sediment erosion occurs when shear stress on the sediment surface is strong enough to initiate particle motion, i.e., erosion threshold (τ_c) is exceeded (Murray 1977; Mitchener and Torfs 1996).

The resistance of sediment to resuspension is influenced by a multitude of biogeochemical features (Grabowski et al.

2011), which are constantly altered by biological activity. The main sediment feature controlling erosion threshold is grain size distribution, but estimating erosion processes of natural sediments has proven to be difficult, because they are often heterogeneous mixtures of different grain sizes characterized by vertical gradients in sediment properties (Amos et al. 1992; Maa et al. 1998, Sanford and Maa 2001; Aberle et al. 2004). In natural sediments, the seafloor sediment composition and consolidation defines the erosion threshold and erosion rate. For example, erosion of a mud and sand mixture depends upon the electrochemical forces of the mud that bind particles together, as well as the physical properties of the sand, such as grain size diameter, but also the packing density, internal structure of the sediment, and stress history (Jacobs et al. 2011). In addition, the chemical and physical characteristics are also constantly modified by benthic macrofauna through feeding, moving, and egestion (Graf and Rosenberg 1997). The effect of benthic macrofauna on sediment erodibility differs depending on the organism's size, abundance, physical features and functioning in and on the sediment (Widdows and Brinsley 2002; Grabowski et al. 2011; Harris et al. 2015, 2016). Moreover, the influence of macrofauna may change with sediment type, due to the natural variation in species abundance and richness in different habitats. Another important biological sediment property, especially in cohesive "muddy" sediment, is a microbially produced biofilm. Biofilms form when individual particles are coated with exopolymeric substances (EPS; Decho 2000; Black et al. 2002). EPS create a smooth biolaminate layer on the sediment surface (Decho 2000; Black et al. 2002) that stabilize the sediment, and if the biofilm is not disturbed by grazing fauna or waves, biolamination of microphytobenthos may develop on sediment surfaces (Reise 2002).

In general, hydrodynamics regulate sediment dispersal, deposition and resuspension (e.g., Jönsson et al. 2005; Green and Coco 2014). Fine sediment particles are often deposited and accumulate in low energy environments forming a "muddy" sediment (Winterwerp and van Kesteren 2004). In contrast, sediment is frequently resuspended in high energy environments, which prevents fine sediment deposition and accumulation (Jönsson et al. 2005; Fagherazzi and Wiberg 2009). Differences in erosion behavior of cohesive "muddy" and noncohesive "sandy" sediments is well acknowledged in the literature. In both sediment types, initial erosion starts with the smallest particles that are easiest to move. This often occurs as aggregate or "floc" erosion in "muddy" sediments (Winterwerp and van Kesteren 2004) and bedload transport of individual grains in "sandy" sediments (Mitchener and Torfs 1996; Jacobs et al. 2011). Sediment erosion and transportation processes, however, are also influenced by the local habitat structure. This can be observed on a small-scale with variations in bed structure (e.g., crest and trough systems, Lanuru et al. 2007) or at a seascape-scale encompassing various habitat types. For example, the

natural variation of vegetated and clear patches in local habitat will affect macrofaunal community composition and local hydrodynamics, and therefore increase the variability in sediment characteristics and erodibility. In subtidal coastal regions, these vegetation patches typically include various species of vascular plants, which provide suitable habitats for benthic fauna and increase sediment stability by dampening water motions and thus sediment erosion (Madsen et al. 2001; James et al. 2004; Nepf 2012). For example, macrophytes may increase sediment stability by reducing shear stress on the sediment surface by approximately 20–80% through changes in flow conditions (Wang et al. 2010). Indeed, natural variations in hydrodynamics, sediment properties, macrofaunal compositions, and vegetation influence erodibility and thus sediment resuspension.

Climate change scenarios predict changes in wind speeds and direction, and frequency of extreme wind events in the future (IPCC 2013). These changes may increase resuspension frequencies and expose new areas to resuspension (Danielsson et al. 2007). Even though erosion threshold is among the key parameters of sediment transport modelling (Sanford 2008), the variability in sediment erodibility and resuspension of natural sediments has remained poorly quantified (Sanford and Maa 2001). Much of the research investigating sediment erosion processes of natural sediments has been done on intertidal flats, and only few of these have tried to encompass a sedimentary gradient with natural variation in environmental variables, especially considering also the effect of biota. Moreover, only little research has accounted for the patchiness of different habitats at a larger seascape scale. Hence, we still lack a comprehensive understanding of sediment characteristics controlling sediment resuspension across sedimentary gradients in subtidal coastal environments. Therefore, it is important to quantify the sediment characteristics and also the large-scale habitat variability controlling this phenomenon.

The main objectives of the present study were to (1) determine the resuspension potential of subtidal sediments across a sedimentary gradient extending the analysis from a small-scale variation within a local habitat to seascape variability across a coastal environment, and (2) identify the sediment characteristics and role of macrofauna in controlling the resuspension potential. In order to explore this, we conducted a field survey across a wide spatial (approx. 19 km) sedimentary gradient in shallow coastal areas of the Baltic Sea. In this area, hydrodynamic forcing is dominated by frequent upwelling and strong wind-wave events (e.g., Haapala 1994; Lehmann & Myrberg 2008; Soomere et al. 2008; Valanko et al. 2015). Based on our current knowledge of erosion processes in "muddy" and "sandy" sediments, we expected the importance of different interactions between physical and biological sediment properties to change along the sedimentary gradient. Previous studies from the study area have shown that the sediment erosion rate is not regulated only by linear or monotonic relationship with hydrodynamic
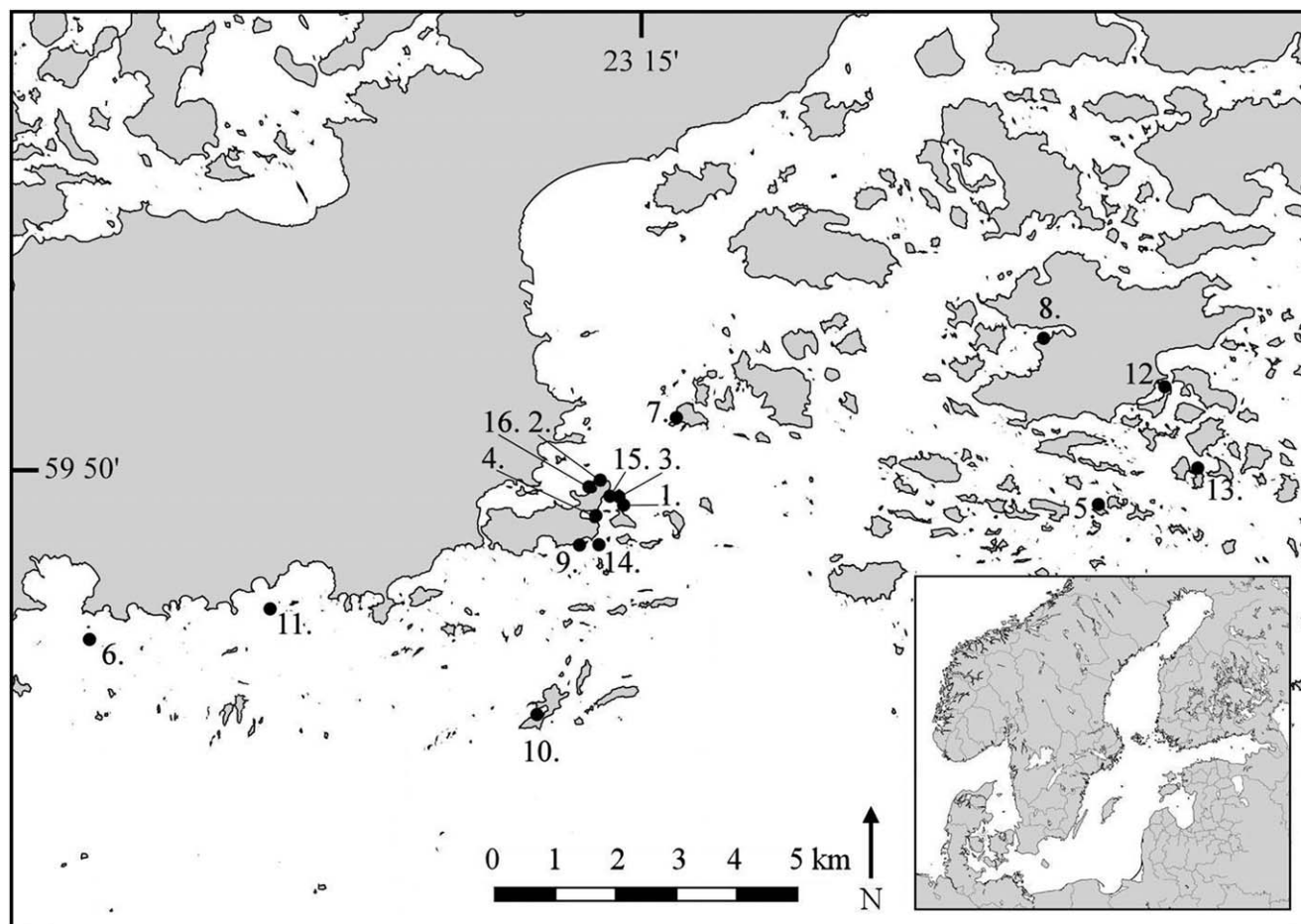
Fig. 1. Sampling locations in the Hanko archipelago, Gulf of Finland (map 1 : 100,000).

forcing, but also depends on the local sediment characteristics and interaction between sedimentary environment and macrofauna (Valanko et al. 2010). Specifically, our focus was to explore the role of benthic macrofauna, and how species richness, abundance and individual size influence the erodibility, while also accounting for variations in habitat characteristics.

Materials and Methods

Study sites

The study was conducted along the north-western coast of the Gulf of Finland in the Baltic Sea (Fig. 1). There are no significant tides in the area, and therefore resuspension events are mainly caused by wind-driven waves and large-scale currents, such as upwelling events (Haapala 1994; Danielsson et al. 2007; Valanko et al. 2010, 2015). Sixteen sites were chosen to encapsulate a sedimentary gradient from "muddy" to "sandy" sediments in shallow (< 4 m), photic and oxygen-rich coastal environments with similar water depth, temperature, oxygen conditions and salinity (Table 1). Sites were sampled during a 4-week period in August and September 2014 encapsulating a gradient from very fine

sediments in sediment accumulation areas to coarser sediments in highly dynamic areas (Supporting Information 1). This gradient encompassed different habitats ranging from low to high macrofaunal species richness, and areas with and without vegetation. Sediment surface texture also varied from biofilm covered muddy sediments to coarse sands with small stones.

Field sampling design

At each site, a 20–30 m semicircle transect was established by SCUBA divers, maximizing the small-scale variation in sediments and vegetation within the site. Four quadrats (0.25 m²) were positioned 4–5 m apart along the transect to capture within site variations in sediment surface features (e.g., bed forms, vegetation, and biofilm coverage). The local habitat inside the quadrats (0 m) and along transect (± 2 m) was videotaped for further analyses of seascape features. An EROMES core (Ø 10 cm, 10 cm depth) was pushed into the sediment and collected from the middle of each quadrat for the determination of erosion potential (see below). Prior to removing the EROMES core, surface sediment samples (0–0.5 cm depth) were collected next to the EROMES core with

Table 1. Near bed environmental data from each sampling location in the Hanko archipelago and the number of quadrats sampled.

Site	Date	Latitude	Longitude	Depth (m)	Temperature (°C)	Oxygen (mg L^{-1})	Salinity	Number of quadrats
1	06 Aug 2014	59 50,853	23 15,379	3.9	22.0	8.8	5.2	4
2	07 Aug 2014	59 51,066	23 14,937	3.2	22.5	8.6	5.2	3
3	09 Aug 2014	59 50,925	23 15,285	3.0	21.8	8.6	5.1	4
4	11 Aug 2014	59 50,749	23 14,897	2.3	22.0	8.2	5.2	4
5	14 Aug 2014	59 51,094	23 23,764	2.6	19.5	8.1	5.1	4
6	15 Aug 2014	59 49,387	23 06,083	3.0	17.8	8.7	5.4	4
7	21 Aug 2014	59 51,658	23 16,225	3.0	16.5	9.4	5.4	4
8	22 Aug 2014	59 52,549	23 22,639	2.9	17.2	9.0	5.1	3
9	25 Aug 2014	59 50,480	23 14,637	3.0	15.3	9.8	5.4	2
10	28 Aug 2014	59 48,949	23 14,059	3.8	14.8	9.9	5.5	4
11	29 Aug 2014	59 49,751	23 09,240	3.2	13.6	10.3	5.7	4
12	01 Sep 2014	59 52,178	23 24,828	1.7	15.4	9.1	5.4	4
13	02 Sep 2014	59 51,469	23 25,486	2.4	14.0	10.1	5.6	4
14	04 Sep 2014	59 50,487	23 14,984	3.4	16.2	9.9	5.6	4
15	05 Sep 2014	59 50,929	23 15,124	3.7	15.3	9.9	5.6	3
16	08 Sep 2014	59 50,998	23 14,745	2.5	16.4	10.2	5.5	4

four syringes (Ø 2.1 cm). After the collection, EROMES cores and syringes were transferred to a water bath at in situ-temperatures. Surface sediment samples were pooled, homogenized, then separated into two subsamples and frozen prior to analyses of sediment characteristics.

Determination of sediment erosion measures

A portable EROMES-device (Schünemann and Kühl 1991) was used to determine sediment resuspension potential measures. The EROMES-device provides a relative measurement of sediment stability by generating an instantaneous turbulence at the sediment surface that initiates sediment particle motion. Hence, although the mechanism by which the turbulence shear is generated does not mimic natural hydrodynamic forcing, it does provide easily replicated relative measures of sediment stability on intact communities allowing across site comparisons. A total of 59 EROMES cores were collected from 16 sites. Water level in the cores were adjusted to 20 cm above the sediment surface by removing excess water slowly and cautiously leaving the sediment-water interface undisturbed and intact. A propeller and an optical backscatter sensor were positioned 3 cm and 6.5 cm above the sediment to generate shear stress and measure turbidity, (respectively), in the EROMES cores. A baffle ring was positioned 1.5 cm above the sediment to prevent rotational water flow. The propeller revolutions have been converted to bed shear stresses using the calibration from quartz sand with known critical shear stress (Schünemann and Kühl 1991; Andersen 2001). The bed shear stress was increased every 2 min by 0.1 N m^{-2} from 0 to 2.0 N m^{-2} and water

samples were collected to calibrate the optical backscatter sensor into suspended solids concentration (SSC) (Andersen 2001; Andersen and Pejrup 2002). Separate SSC calibrations were made for each site ($R^2 = 0.87$–0.99, $n = 4$–22). Erosion rates (g m^{-2} s^{-1}) were then calculated from the time derivate of SSC in every bed shear stress interval, and used to determinate the resuspension potential measures. The erosion threshold (τ_c; N m^{-2}) was defined at the erosion rate of 0.1 g m^{-2} s^{-1} (Andersen 2001; Andersen et al. 2005), and was equal to initial bed erosion occurring after the erosion of unconsolidated fine surface material. The erosion rate (ER; g m^{-2} s^{-1}) describes the quantity of eroding sediment at a fixed bed shear stress at 0.5 N m^{-2} (Andersen 2001; Andersen et al. 2005; Lumborg et al. 2006; Harris et al. 2016). The erosion constant (m_e; g N^{-1} s^{-1}) was used to analyze the change in erosion rate with increasing bed shear stress (Mitchener and Torfs 1996). To estimate m_e, erosion rates were plotted against bed shear stress and m_e was derived from the slope between 1.0 and 1.6 N m^{-2} (Harris et al. 2015), the range representing erosion process after the initial erosion. Since the τ_c is related to the initial motion of particles, high values refer to a more stable sediment, with greater shear stress needed to exceed the τ_c. In contrast, high ER represents a less stable sediment, as sediment is eroded more rapidly from the bed. Similarly, high m_e indicates a more rapid erosion rate with increasing bed shear stress. The τ_c and ER describe the early stage of erosion occurring in the surface layer of the sediment, whereas m_e describes later stage erosion of subsurface sediments, which occurs after the surface layer has been eroded.

Environmental variables

Chlorophyll *a* and phaeopigment concentrations were analyzed spectrophotometrically at 665 and 750 nm wavelengths from lyophilized subsamples after acetone extraction and 24 h incubation at 4°C in darkness. Prior to spectrophotometric measurement, samples were centrifuged at 3000 rpm (10 min at 20°C) and measured before and after acidification (calculations followed Lorenzen 1967). Sediment water content was calculated as the difference between wet weight and dry weight (105°C for 12 h) and organic content was determined using loss-on-ignition (450°C for 4 h) from a fresh subsample. For estimates of dry bulk density (g cm^{-3}), the sediment particle density was assumed to be 2.65 g cm^{-3} (Mehta and Lee 1994; Avnimelech et al. 2001) and water density 1.0 g cm^{-3}, and calculations followed Roberts et al. 1998. For the grain size samples, large shell fragments were removed and the samples were treated with hydrogen peroxide (H_2O_2, 6%) to dissolve the organic material, sieved (63, 250, 500 μm) and the percent of each size fractions measured. After the resuspension potential measurements, the EROMES cores were sieved with a 500 μm mesh and benthic macrofauna extracted, stored in 70% ethanol, stained (Rose Bengal) and identified to the lowest taxonomic level practical (usually species). Last, vegetation coverage (%) inside each quadrat (vegetation coverage at 0 m) and at 2 m either side along the transect in both directions (vegetation coverage at ± 2 m) was determined from the videos.

Statistical analysis

Despite our inclusion of sites, samples represent a sedimentary gradient and were analyzed individually instead of site-specific analysis. Non-metric multi-dimensional scaling (MDS) was used to examine and visualize patterns in the sedimentary environment. The MDS plot was based on a Euclidean distance resemblance matrix of fourth-root transformed and normalized sediment data (median grain size, clay and mud content, dry bulk density, porosity, water content and organic content). In an initial review of data, samples split into two clusters in the MDS plot (Fig. 2). These clusters (hereafter "muddy" and "sandy" sediments) were confirmed to be significantly different ($p \leq 0.001$) with a pair-wise PERMANOVA analysis (9999 permutations). Based on the knowledge of different erosion behaviors of "muddy" and "sandy" sediment, they were analyzed and treated separately. To investigate significant ($p \leq 0.05$) differences in univariate measures of macrofaunal community composition and vegetation parameters between "muddy" and "sandy" sediments, separate Bray-Curtis resemblance matrices were computed for species richness, macrofaunal abundance and biomass, vegetation parameters, and analyzed with the pair-wise PERMANOVA analysis based on 9999 permutations. In addition, separate Euclidean distance resemblance matrixes were
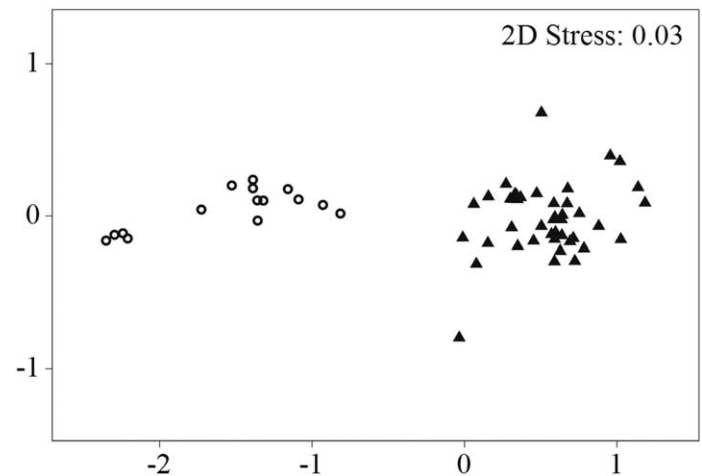
Fig. 2. Two-dimensional MDS plot of the sedimentary environment. Open circles are replicates from "muddy" sediments ($n = 15$) and closed triangles are replicates from "sandy" sediments ($n = 44$).

computed for each resuspension potential measures and analyzed with the pair-wise PERMANOVA (9999 permutations) to examine if resuspension potential measures differ significantly ($p \leq 0.05$) between sediment types.

Distance-based linear modeling (DistLM) was used to analyze how much variation in resuspension potential measures could be explained by environmental variables. Separate Euclidean distance resemblance matrixes were computed with permutation techniques for each resuspension potential measure (τ_c, ER, and m_e). Significant ($p \leq 0.05$) and marginally significant ($p \leq 0.1$) single predictors were identified using "marginal" tests (9999 permutations). "Step-wise" selection procedure was then used to analyze the combination of significant predictor variables that could explain the greatest percent variation in resuspension potential measures. Square and fourth root transformations were used when necessary to diminish the influence of outliers or skewness of the predictor variables, and all of them were normalized before DistLM analysis. Predictor variables were chosen based on correlation matrices (Supplementary information 2 and 3) and variables that were highly correlated after transformations (Pearson's $r \geq 0.8$) were excluded. As a model selection, an Akaike's Information Criterion (AICc), with a modification for sample size with relatively high number of predictor variables (Clarke and Gorley 2015) was used. The AICc explores the combination of predictor variables that could explain most of the variation in the data with lowest number of predictor variables. All statistical analyses were accomplished with the PRIMER 7 PERMANOVA+.

Results

Environmental variables

The MDS plot showed that the "muddy" and "sandy" sediments were substantially different, yet there was high

Table 2. Summary of sediment properties, microalgal biomass, species richness, macrofaunal biomass and abundance, and sediment resuspension potential (erosion threshold [τ_c], erosion rate [ER]. and erosion constant [m_e]) in "muddy" and "sandy" sediments.

	'Muddy' sediments ($n = 15$)		'Sandy' sediments ($n = 44$)	
Sediment properties				
Median particle size (μm)	47	(21–116)	312	(127–845)
Clay content (%)	9.9	(4.2–13.6)	0.5	(0.0–1.6)
Mud content (%)	59.3	(25.2–81.9)	2.8	(0.2–9.8)
Dry bulk density (g cm^{-3})	1.3	(1.1–1.5)	1.9	(1.5–2.1)
Water content (%)	62.3	(46.2–87.4)	23.6	(17.0–43.4)
Porosity	0.6	(0.5–0.9)	0.2	(0.2–0.4)
Organic content (%)	7.4	(2.8–17.9)	0.9	(0.2–4.0)
Microalgal biomass (μg g^{-1})				
Chlorophyll *a*	39.7	(12.6–99.9)	17.7	(3.5–38.6)
Phaeopigment	24.3	(9.0–63.2)	1.6	(0.0–9.2)
Macrofauna				
Species richness (ind. core^{-1})	3	(1–4)	5	(2–9)
Biomass (g core^{-1})	0.3	(0.0–1.2)	0.7	(0.0–3.2)
Abundance (ind core^{-1})	18	(1–43)	46	(12–108)
Hydrobiidae	7	(0–28)	24	(0–83)
Pygospio elegans	—		0	(0–6)
Oligochaeta	1	(0–3)	2	(0–9)
Marenzelleria sp.	1	(0–6)	3	(0–13)
Hediste diversicolor	0	(0–2)	2	(0–9)
Macoma balthica	9	(0–23)	11	(0–63)
Vegetation coverage (%)				
0 m	2	(0–10)	21	(0–72)
$\pm$ 2 m	3	(0–14)	24	(2–69)
Resuspension potential				
τ_c (N m^{-2})	0.55	(0.39–0.81)	0.88	(0.45–1.39)
ER (g m^{-2} s^{-1})	0.12	(0.01–0.33)	0.04	(0.01–0.14)
m_e (g N^{-1} s^{-1})	5.55	(2.90–8.91)	3.21	(0.05–17.43)

Values are the average and range (min–max) of the environmental variables and resuspension potential measures.

variation within the two sediment types (Fig. 2). Median grain size (D$_{50}$) in "muddy" sediments ranged between 21 and 116 μm and in "sandy" sediments between 127 and 845 μm (Table 2). "Muddy" sediments had greater proportion of fine particles (clay 4.2–13.6% and mud 25.2–81.9%) and higher water content (46.2–87.4%). "Sandy" sediments were more consolidated and had higher dry bulk density (1.5–2.1 g cm^{-3}), but lower organic content (0.2–4.0%) and porosity (0.2–0.4) (Table 2). The surfaces in the muddiest sediments were covered with visible biofilms, whereas ripple marks were observed in sandiest sediments, indicating that a

variation in hydrodynamic conditions (from sheltered to exposed environments) was also included into the study (Supporting Information 1). Microalgal biomass increased with increasing mud content in "muddy" sediments, but not in "sandy" sediments (Supporting Information 2 and 3). As expected, the highest concentrations of microalgal biomass were found in "muddy" sediments, yet there was also some overlap between the sediment types.

Gastropoda *Hydrobiidae* and the bivalve *Macoma balthica* were the most abundant species in both "muddy" and "sandy" sediments. The polychaete *Pygospio elegans* was found only in "sandy" sediments. Species richness, macrofaunal abundance and biomass were significantly lower in "muddy" sediments compared to "sandy" sediments (PERMANOVA, $p < 0.05$). Vegetation coverage was consistently lower in "muddy" sediments compared to the "sandy" sediments (Table 2). On the larger habitat scale, only "sandy" sediments consistently had vegetation $\pm$ 2 m distance from the sampled quadrat. The differences in vegetation coverage were significant (PERMANOVA, $p < 0.05$) between the sediment types. Typical submerged aquatic vegetation species were *Potamogeton pectinatus* and *Potamogeton perfoliatus* in "muddy" sediments, and *Ceratophyllum demersum* and *P. perfoliatus* and *Zostera marina* in "sandy" sediments (Gustafsson and Norkko 2016).

Resuspension potential measures

Generally, τ_c was lower and ER and m_e were higher in "muddy" sediments compared to "sandy" sediments (Table 2), indicating that sediment was eroded at lower shear stress in "muddy" sediments compared to "sandy" sediments. The highest ER were found in "muddy" sediments (0.33 g m^{-2} s^{-1}), which was twofold higher compared to "sandy" sediments (0.14 g m^{-2} s^{-1}). Interestingly, in some "sandy" sediments a few m_e values reached the substantially higher values than measured in "muddy" sediments (Table 2). Although τ_c and ER were significantly different (pairwise PERMANOVA, $p \leq 0.05$) between "muddy" and "sandy" sediment, all resuspension potential measures overlapped across sediment types.

In "muddy" sediments, τ_c increased with decreasing particle size as mud and clay content increased (Supporting Information 2 and 3). Accordingly, ER and m_e increased with increasing particle size and decreasing mud and clay content. Median particle size and dry bulk density were positively correlated in "muddy" sediments indicating that sediment consolidation was lower in the muddiest sediments and thus they were eroded more easily. Most of the variation in τ_c and in ER were explained by median particle size (42% and 38%, respectively), (Fig. 3a,b), whereas most of the variation in m_e was explained by dry bulk density (53%) (Fig. 3c). Also the abundance of Oligochaeta was a significant single predictor, explaining 34% and 28% of the variation in τ_c and ER, respectively (Table 3). ER was marginally significantly correlated with higher vegetation coverage at 0 and $\pm$ 2 m, suggesting
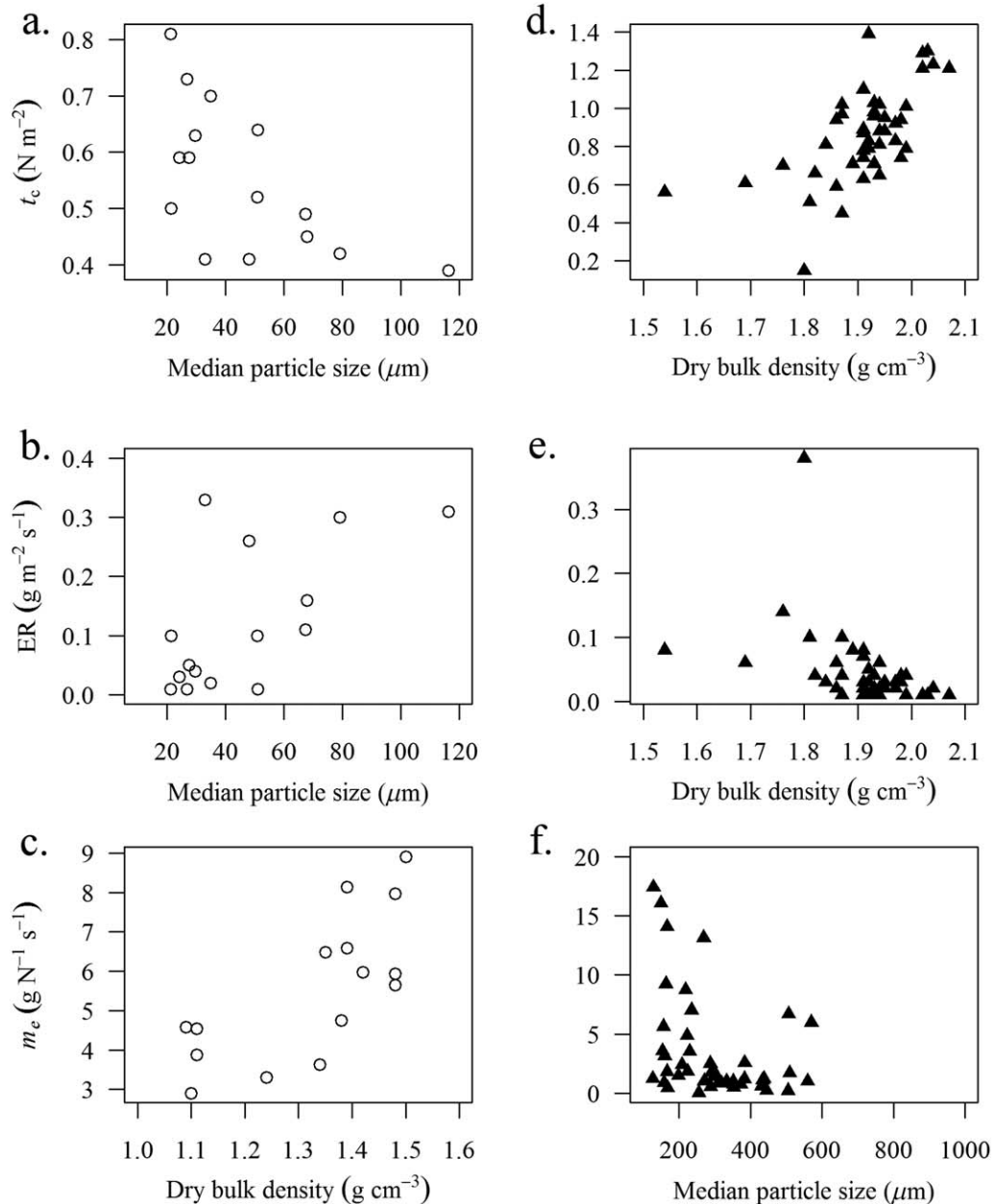
Fig. 3. The main significant single predictors for resuspension potential measures in "muddy" (**a–c**) and "sandy" sediments (**d–f**). Erosion threshold (τ_c; **a**) and erosion rate (ER; **b**) were correlated with median particle size ($R^2 = 42\%$ and 38%, respectively), and erosion constant (m_e; **c**) was correlated with dry bulk density ($R^2 = 53\%$) in "muddy" sediments. In "sandy" sediments, erosion threshold (τ_c; **d**) and erosion rate (ER; **e**) were correlated with dry bulk density ($R^2 = 36\%$ and 31%, respectively), and erosion constant (m_e; **f**) was correlated with median particle size ($R^2 = 15\%$).

that in "muddy" sediments, ER is higher in vegetated habitats. Chlorophyll *a* concentration explained 22% of the total variation in ER and 20% of the total variation in m_e (Table 3). Both ER and m_e decreased with increasing chlorophyll *a* concentration, indicating a stabilizing effect from the biofilm. However, the correlation between ER and chlorophyll *a* was only marginally significant (Table 3). ER and m_e increased with decreasing organic content, while ER increased with the abundance of *Marenzelleria*, and m_e with the abundance of macrofauna in

general, but also with the abundance of Oligochaeta and *M. balthica*, indicating that the presence of macrofauna and biofilm absence were destabilizing the sediment. Nevertheless, the best single predictor of m_e was dry bulk density, which explained 53% of the total variation (Table 3). The DistLM analysis was used to determine the best combination of predictor variables explaining the greatest percent of the variation in the resuspension potential measures. Although *M. balthica* was only a marginally significant single predictor of τ_c

Table 3. Proportion of variation (prop.) explained by each significantly correlated environmental variable in resuspension potential measures (marginal DistLM).

		Variable	Pseudo-*F*	Prop.		
"Muddy" sediments	τ_c	Median particle size (μm)	9.45	0.42	***	(−)
($n = 15$)		Oligochaeta (ind core^{-1})	6.85	0.34	**	(+)
		M. balthica (ind core^{-1})	3.63	0.22	*	(+)
		Marenzelleria (ind core^{-1})	2.48	0.16	*	(−)
	ER	Median particle size (μm)	7.97	0.38	**	(+)
		Oligochaeta (ind core^{-1})	5.17	0.28	**	(−)
		Vegetation coverage 0 m (%)	3.61	0.22	*	(+)
		Vegetation coverage ± 2 m (%)	3.43	0.21	*	(+)
		Chlorophyll *a* (μg g^{-1})	3.19	0.20	*	(−)
		Marenzelleria (ind core^{-1})	2.84	0.18	*	(+)
		Organic content (%)	2.40	0.16	*	(−)
	m_e	Dry bulk density (g cm^{-3})	14.81	0.53	***	(+)
		Organic content (%)	10.29	0.44	***	(−)
		Phaeopigment (μg g^{-1})	7.77	0.37	**	(−)
		M. balthica (ind core^{-1})	7.44	0.36	**	(+)
		Macrofaunal abundance (ind core^{-1})	6.87	0.35	**	(+)
		Chlorophyll *a* (μg g^{-1})	6.28	0.33	**	(−)
		Median particle size (μm)	6.14	0.32	**	(+)
		Oligochaeta (ind core^{-1})	2.83	0.18	*	(+)
"Sandy" sediments	τ_c	Dry bulk density (g cm^{-3})	23.82	0.36	***	(+)
($n = 44$)		Organic content (%)	10.39	0.20	***	(−)
		Species richness	8.97	0.18	***	(+)
		P. elegans (ind core^{-1})	6.59	0.14	**	(+)
		Vegetation coverage 0 m (%)	4.10	0.09	**	(+)
		Oligochaeta (ind core^{-1})	3.82	0.08	*	(+)
		H. diversicolor (ind core^{-1})	3.30	0.07	*	(+)
		Phaeopigment (μg g^{-1})	3.40	0.07	*	(−)
		Chlorophyll *a* (μg g^{-1})	2.32	0.05	*	(−)
	ER	Dry bulk density (g cm^{-3})	19.21	0.31	***	(−)
		Vegetation coverage 0 m (%)	9.11	0.18	**	(−)
		Organic content (%)	7.56	0.15	**	(+)
		Median particle size (μm)	2.68	0.06	*	(−)
	m_e	Median particle size (μm)	7.30	0.15	**	(−)
		Macrofaunal biomass	4.30	0.09	**	(−)
		Vegetation coverage ± 2 m (%)	3.98	0.09	**	(−)
		Vegetation coverage 0 m (%)	3.65	0.08	*	(−)
		Species richness	2.48	0.06	*	(−)

The significance levels considered are *$p \leq 0.1$; **$p \leq 0.05$; ***$p \leq 0.01$. The direction of the correlation is given in parentheses.

in "muddy" sediments, the best combination of predictor variables included median particle size and abundance of *M. balthica*, explaining 68% of the total variation (Table 4). Median particle size was also included into the best model of ER, together with Oligochaeta explaining 56% of the total variation (Table 4). A combination of dry bulk density and *M. balthica* abundance explained 66% of the total variation in m_e, but

the combination was only marginally significant, whereas dry bulk density remained the single significant predictor (Table 4).

In "sandy" sediments, the influence of sediment properties together with the local habitat structure was apparent. The best single predictor of τ_c was dry bulk density, which explained 36% of the variation (Fig. 3d). While organic content, chlorophyll *a* and phaeopigment concentration decreased, τ_c increased,

Table 4. The best combination of predictor variables explaining greatest percent of the variation in sediment resuspension measures in "muddy" and "sandy" sediments.

		Variable	AICc	Prop.	Cum.	
"Muddy" sediments ($n = 15$)	τ_c	Median particle size	−65.31	0.42	0.42	***
		M. balthica	−71.16	0.26	0.68	***
	ER	Median particle size	−67.08	0.38	0.38	**
		Oligochaeta	−69.00	0.18	0.56	**
	m_e	Dry bulk density	10.85	0.53	0.53	***
		M. balthica	9.45	0.12	0.66	*
"Sandy" sediments ($n = 44$)	τ_c	Dry bulk density	−150.58	0.36	0.36	***
		Species richness	−154.99	0.09	0.45	***
		Vegetation coverage 0 m	−155.19	0.03	0.48	*
		P. elegans	−155.59	0.03	0.52	*
	ER	Dry bulk density	−322.67	0.31	0.31	***
		Vegetation coverage 0 m	−328.59	0.12	0.43	***
		Median particle size	−329.87	0.05	0.48	*
	m_e	Median particle size	120.28	0.15	0.15	***
		Species richness	115.65	0.12	0.27	***
		Vegetation coverage 0 m	113.80	0.07	0.34	**
		Macrofaunal biomass	113.00	0.05	0.39	*

"Step-wise" model selection was based on the corrected Akaike information criterion (AICc). Proportion of variation explained by individual predictors (prop.) and cumulatively (cum.) are shown. The significance levels considered are * $p \leq 0.1$; ** $p \leq 0.05$; *** $p \leq 0.01$.

together with species richness and abundance of *P. elegans*, Oligochaeta and *Hediste diversicolor*. Only organic content, species richness, and abundance of *P. elegans* were significant single predictors, explaining 20%, 18%, and 14% of the total variation in τ_c, respectively, (Table 3). Vegetation coverage at 0 m explained 9% of the total variation in τ_c, suggesting more stable sediments in vegetated habitats adjacent to bare patches. This was also seen in ER, where ER decreased with increasing vegetation coverage at 0 m. Vegetation coverage at 0 m was significantly correlated and explained 18% of the total variation in ER. However, the best single predictor of ER was dry bulk density, explaining 31% of the total variation (Fig. 3e). In addition, ER increased with increasing organic content, which explained 15% of the total variation. In contrast to "muddy" sediments, τ_c increased and ER and m_e decreased in "sandy" sediments with increasing median particle size and decreasing mud and clay content. Median particle size was only a marginally significant predictor of ER explaining 6% of the total variation, but it was the best single predictor in m_e explaining 15% of the total variation (Fig. 3f). Further, macrofaunal biomass was a significant predictor of m_e, explaining 9% of the total variation, and species richness was a marginally significant predictor, explaining 6% of the total variation. Vegetation coverage both at 0 and ± 2 m were marginally significant predictors explaining 8% and 9% of the total variation in m_e, respectively. In "sandy" sediments, the vegetation coverage at 0 m was included into all combinations of best

predictors in resuspension potential measures (Table 4). Dry bulk density, together with the species richness, vegetation coverage at 0 m and the abundance of *P. elegans* explained 52% of the total variation in τ_c (Table 4). However, the combination was only marginally significant, when in fact, the highly significant combination of dry bulk density and species richness explained most of the total variation (45%). The best significant combination of predictor variables of ER were dry bulk density and vegetation coverage at 0 m, which together explained 43% of the total variation (Table 4). Including median particle size, the explanatory rate reached 48%, but this combination was marginally significant. When considering m_e, the best combination included median particle size, species richness, and vegetation coverage at 0 m and macrofaunal biomass, which together explained 39% of the total variation (Table 4). When the marginally significant predictor macrofaunal biomass was removed, this explanatory rate reached 34%.

Discussion

In this study, we have quantified how physical and biological sediment characteristics, including elements of local habitat structure and macrofauna, influence sediment erodibility and resuspension in a submerged coastal environment. Our study encompassed 16 different sampling sites, with 59 samples across a broad-scale sedimentary gradient. The samples diverged into two groups of "muddy" and "sandy" sediments

with considerable variation in environmental variables both between and within these two sediment types. Accounting for the physical properties of the sediment in resuspension potential measures, we sought to determine the role of local habitat structure and macrofauna. Overall, physical sediment properties explained 38–42% and 15–36% of the total variation in resuspension potential measures of "muddy" and "sandy" sediments, while macrofauna and vegetation explained additional 15–24% and 12–26%, respectively, (Table 4). The seafloor landscape is highly variable in time and space, and our results suggest that sediment resuspension potential are affected by different factors, depending on the local sedimentary environment, resident benthic communities and habitat structure.

In general, cohesive behavior typically occurs when the sediment clay content is 3 to 15% of the total sediment weight (Mitchener and Torfs 1996). In our study, the clay content in "muddy" sediments varied from 4 to 14% (Table 2), indicating that erosion processes in these sediments were mainly regulated by cohesive forces. From physical sediment properties, median particle size was found to be the most important predictor for τ_c and ER in "muddy" sediments explaining 42% and 38% of the total variation, respectively. Clay and mud content were positively correlated with τ_c and negatively correlated with ER, indicating the stabilizing effect of very fine particles by cohesion and adhesion (Kamphuis and Hall 1983; Grabowski et al. 2011). This was further supported by the significant negative correlation between τ_c and median particle size (Table 3), also noted by Roberts et al. (1998). The negative correlation between τ_c and median particle size may also illustrate sediment erosion as aggregates. Very fine particles can form aggregates that may reach mean diameters of 2000 μm (Thomsen and Gust 2000) and can increase bed resistance against erosion. Dry bulk density explained 53% of the total variation in m_e. Although previous findings suggest that erosion rates generally decrease as the dry bulk density increases (Roberts et al. 1998), our results, obtained from natural "muddy" sediments show a different pattern. The positive correlation between m_e and dry bulk density in "muddy" sediments suggests that the sub-surface erosion was more rapid as the dry bulk density increased. Since dry bulk density describes sediment consolidation (i.e., sediments "hardness" against erosion) and it increases with decreasing water content and porosity, erosion should decrease with increasing clay content or particle size (i.e., more consolidated bed) in "muddy" sediments. Typically, bulk density is lower and τ_c higher in consolidated clays than in fine sands (Grabowski et al. 2011), which can explain our results. Our results may also indicate that the sediment was eroded more easily in the transitional region where cohesive forces were insignificant yet particles were still relatively small. Additionally, studies considering the relationship between bulk density and bed erosion are often made with bulk densities ≥ 1.65 g cm^{-3}, whereas the dry bulk densities in our results from the "muddy" sediments

were from the surface layer of sediment with a range of 1.1–1.5 g cm^{-3}, and thus markedly lower. However, the dry bulk density calculations in our study were based on the density of quartz particles, while sediments containing a significant fraction of organic matter may have lower particle density (Avnimelech et al. 2001). Nevertheless, to enable consistency across "muddy" and "sandy" sediments, the same particle density was used in all calculations.

Both *M. balthica* and Oligochaeta impacted sediment erosion in "muddy" sediments. The abundance of *M. balthica* added 26% and 12% to the cumulative explanation rate (τ_c and m_e, respectively), and Oligochaeta added 18% in ER (Table 4). Interestingly, both τ_c and m_e were positively correlated with *M. balthica*, indicating a somewhat contradicting effect on sediment stability. Our results suggest that *M. balthica* stabilize the surface sediment, but destabilize the sub-surface sediment after initial erosion. The destabilizing impact of *M. balthica* in the later stage of the erosion process may result from the organisms' functioning in the sediment (e.g., burrowing, deposit-feeding), which alters sediment properties and structure, but also from microscale roughness created by organisms' shells and burrows. In general, deposit-feeding macrofauna reduce the stabilizing effect of microalgae and biofilms on the surface of the "muddy" sediments by grazing and subsequently decreasing sediment cohesiveness (Austen et al. 1999; Lelieveld et al. 2004; Weerman et al. 2011; Pratt et al. 2014), and therefore we would have expected a destabilizing effect of *M. balthica* on the initial erosion of the surface sediment. Further, both τ_c and the abundance of *M. balthica* were negatively correlated with vegetation coverage at 0 m (Supplementary information 3), which suggest that the sediment was eroded more easily in vegetated patches with lower abundance of *M. balthica*. Similarly, abundance of Oligochaeta was negatively correlated with ER and vegetation at 0 m, but ER was positively correlated with vegetation at 0 m. This suggest that erosion rates were higher in vegetated patches with low abundance of Oligochaeta. Vegetation efficiently dampens wave motions, traps sediment and decreases resuspension (Madsen et al. 2001; James et al. 2004; Nepf 2012), and therefore may enhance sedimentation and the accumulation of suspended solids (i.e., a "fluff layer") on the sediment surface (Nepf 2012), which then are easily eroded.

In "sandy" sediments, dry bulk density and median particle size were also found to be the best predictors of resuspension potential measures. Dry bulk density explained 36 and 31% of the total variation in τ_c and ER, respectively. Contrasting to "muddy" sediments, dry bulk density was positively correlated with τ_c and negatively correlated with ER in "sandy" sediments. The density of the bed increases with depth as water content decreases (Mitchener and Torfs 1996), and our results indicate that more compacted sediment was more resistant to erosion. Median particle size is often used as a single predictor of initial bed erosion, but interestingly we did not observe a significant correlation between τ_c and median particle size.

Instead, median particle size explained 15% of the total variation in m_e, suggesting that larger particles stabilize the subsurface erosion in "sandy" sediments. This was also seen in ER, where median particle size added 5% to the cumulative explanation rate (Table 4). The negative correlations between τ_c and fine fractions of the sediment (i.e., clay, mud and organic matter) suggest a presence of easily eroded fine particles ("fluff layer") on the sediment surface, which may explain why median particle size was not a significant predictor for the initial erosion, but instead dry bulk density was.

When considering biota in "sandy" sediments, the vegetation at 0 m was found to be a key predictor for sediment resuspension as it increased cumulative explanatory power of all resuspension potential measures by 3–12% (Table 4). In contrast to "muddy" sediments, vegetated patches increased stability in "sandy" sediments, i.e., τ_c was positively and ER and m_e were negatively correlated with vegetation at 0 m. The stabilizing effect of roots and rhizomes on sediment is well acknowledged in the literature (e.g., Le Hir et al. 2007; Grabowski et al. 2011). Vegetated patches also provide habitats for microbial communities, which in turn can produce a stabilizing biofilm. We also found a positive correlation between τ_c and the abundance of the polychaete *P. elegans*, suggesting that it stabilizes the surface sediments. *P.elegans* constructs mucus coated sand tubes, which bind sediment particles together (Bolam and Fernandes 2003) and also maintain microhabitats for microbial communities. In addition, species richness added 15% and macrofaunal biomass 5% to the cumulative explanation rate in m_e. Since the net effect of benthic macrofauna on sediment erodibility differs depending organism's size, abundance, physical features and functioning, generalizations are difficult to make. Here, species richness is probably related to sediment heterogeneity of diverse habitats and covariation of multiple environmental variables. Additionally, the magnitude of functioning is higher for larger individuals, e.g., they feed and egest more, produce greater amounts of mucus and EPS and also construct larger and deeper biogenic structures (Norkko et al. 2013). Therefore, larger animals will likely play a central role in sediment erodibility in rough, high energy environments.

In order to put our resuspension potential measures to a context, we converted our results of erosion threshold to critical friction velocities (1.96–2.84 cm s^{-1} for "muddy" sediments and 2.11–3.73 cm s^{-1} for "sandy" sediments). These values are in the same range as estimated friction velocities in previous studies from the area (1.25–3.58 cm s^{-1}, Valanko 2012). Hydrodynamic forcing in the study area is regulated by upwelling and wind-wave events (Haapala 1994; Lehmann & Myrberg 2008) and previous studies have shown that resuspension is a frequent phenomenon in the area (Valanko et al. 2010, 2015).

In this study, we have shown that local habitat structure plays an important role in sediment erodibility and resuspension potential. The mosaic of bare sediment and vegetated patches at the seascape level not only created diverse habitats for macrofaunal communities, but also influenced the sedimentary environment and local hydrodynamics. After accounting for the physical sediment properties, we found that the influence of benthic macrofauna on resuspension potential measures was higher in "muddy" sediments compared to "sandy" sediments. Nevertheless, species richness and vegetation, and thus habitat diversity were important predictors of resuspension potential also in "sandy" sediments. Sediment erodibility and resuspension potential in natural sediments fluctuate from small scale variations within the habitat mosaics to larger spatial scale variations across habitats and sedimentary gradients. Our results underline the importance of biota to resuspension potential measures in spatially variable environments.

Despite the significance of these findings, addressing temporal variation was beyond the scope of this study, and future investigations are needed to analyze how biotic variables (e.g., microbial biomass, vegetation and macrofauna) change seasonally to affect resuspension dynamics in submerged, coastal environments. For example, temperature is a variable that affects all biological processes including the microbial processes central for the cohesive forces affecting resuspension (e.g., EPS, microphytobenthic biomass). Across our study locations, we encountered an 8°C difference in temperature from the sheltered muddy to the exposed sandy sites. Our spatial study design could not account for the relative importance of temperature in affecting resuspension processes, which further highlights the importance of conducting seasonal studies to resolve the influence of temperature and seasonal succession in biology in affecting these processes.

Coastal areas are highly valuable environments for both marine and human life (Levin et al. 2001) and threatened by biodiversity loss, eutrophication, pollutants, erosion and anthropogenic actions. Future challenges include climate change that has been predicted to increase the frequency of extreme events, such as strong wind-waves and storms (Danielsson et al. 2007; IPCC 2013). In addition, prevailing wind directions are predicted to change, therefore exposing new areas for erosion and resuspension. This is particularly important in shallow coastal areas where hydrodynamic forcing regulate sediment erosion and transportation processes. For example, coastal erosion is a major problem in many areas and it will need more attention in the future (Zhang et al. 2004). Therefore, understanding sediment transport processes is not only important for modeling approaches, but also for engineering and other disciplines addressing these challenges.

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Conflict of Interest

None declared.