



Temporal Variation in Resuspension Potential and Associated Nutrient Dynamics in Shallow Coastal Environments

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Abstract

Sediment resuspension may play a major role in sediment-water exchange of nutrients, matter and energy in coastal areas where waves and currents dominate sediment transport. Biogeochemical sediment properties regulate sediment erodibility, but there is only limited knowledge of how temporal variability in environmental variables is reflected in the resuspension potential, especially for subtidal habitats. Further, the significance of resuspension on nutrient fluxes in coastal environments has remained unclear as contradicting results have been reported. Here we quantified the temporal variation in resuspension potential metrics (erosion threshold (τ_c ; N m^{-2}) and erosion constant (m_c ; $\text{g N}^{-1} \text{s}^{-1}$)) and associated nutrient fluxes from three sites in the Hanko archipelago (Finland) using a core-based erosion device (EROMES). The sites were sampled bi-monthly from April to December. We also quantified the temporal variation in biogeochemical sediment properties at each site. The τ_c exhibited the clearest temporal pattern in muddy sediment, where the coefficient of variation (= 67) was two to three times higher than the mixed (= 29) and sandy (= 16) sediments. Dry bulk density was the best predictor for sediment erodibility at all sites explaining 26–46% of the temporal variation in τ_c despite its limited variability at sandier sites. In addition, temporal variations in the macrofaunal community were important predictors of muddy sediment erodibility and therefore community dynamics need to be considered in sediment transport studies. All sites were potential nutrient sources, yet the overall role of sediment resuspension on nutrient release from the sediments was small.

Keywords Coastal areas · Sediment properties · Erosion threshold · Erodibility · Nutrients · Baltic Sea

Introduction

Benthic-pelagic coupling plays an important role for the productivity of coastal ecosystems (Griffiths et al. 2017). In shallow areas, episodic resuspension events may dominate the sediment-water exchange of nutrients, matter and energy,

therefore impacting on water quality, pollutant and organism dispersal, and biogeochemical cycles (e.g. Alongi and McKinnon 2005; Lawson et al. 2007; Warrick 2012; Edge et al. 2015). For example, remineralization of organic matter in the sediment enriches pore waters with nutrients and may be rapidly mixed with the water column during resuspension influencing coastal primary production. Moreover, sediment resuspension also impacts redox conditions by oxygenating reduced sediments affecting sediment biogeochemistry (Ahmerkamp et al. 2015). As sediments are potential nutrient sources for primary producers, it is particularly important to account for processes that influence sediment-water exchange rates of nutrients in estuarine and coastal ecosystems, where eutrophication is a worldwide problem (e.g. McGlathery et al. 2007; Diaz and Rosenberg 2008).

Sediment resuspension occurs when shear stress from wind-waves and/or currents exceeds the erosion threshold on the sediment surface and initiates particle motion (e.g. Miller et al. 1977; Lick et al. 2004). The erosion threshold is governed not only by grain size distribution but complex biophysical interactions that include sedimentation history, local

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habitat structure (e.g. vegetated patches) and the resident benthic flora and fauna whose activities can stabilize or destabilize the sediment (e.g. Black et al. 2002; Harris et al. 2015, 2016; Joensuu et al. 2018). Despite growing insights into the variables that affect sediment resuspension, our understanding of spatial-temporal variability remains limited; for example, the relative importance of the different, site-specific and biophysical interactions that determine sediment stability are likely to vary seasonally with environmental conditions.

Temperature has a direct influence on sediment erodibility by changing physical fluid properties (e.g. decreasing pore water viscosity (Winterwerp and van Kesteren 2004)) but also indirectly through effects on the activity levels and ecology of organisms. Given the seasonal succession of benthic communities, variations in production of organic matter (e.g. algal blooms), vegetation and bacterial growth, the indirect effects of temperature on sediment erodibility may be pivotal, albeit complex, and poorly understood. For example, a microbial biofilm that may cover extensive areas during warmer summer months is a seasonally important variable that can have a major influence on sediment erodibility (e.g. Holland et al. 1974; Yallop et al. 2000; Gerbersdorf et al. 2008). Biofilms are formed by microbial secretion of extracellular polymeric substances (EPS), which coats particles and sticks them together, therefore creating a smooth, biolaminar layer on the bed in calm conditions (e.g. Decho 2000; Reise 2002; Tolhurst et al. 2008). Also diatoms, which often dominate both pelagic and benthic spring blooms can form a stabilizing layer on the sediment surface (Reise 2002). On the other hand, the role of benthic macrofauna on the sediment stability may also depend on the temporal changes in their abundance, life stage and activity. For example, the dominance of the gastropod *Hydrobia ulvae* during summer months may reduce sediment stability because of higher grazing activity, egestion rate and increased production of faecal pellets in warmer temperatures (Austen et al. 1999; Andersen et al. 2002).

Most of the previous studies that have addressed temporal variation in the sediment erodibility in the northern hemisphere have been conducted on intertidal mudflats (e.g. Widdows et al. 2000; Andersen 2001; Friend et al. 2005; Wiberg et al. 2013), except one in riverine sediments (Grabowski et al. 2012). Previous studies have found that the temporal variation in sediment erodibility of intertidal flats is regulated not only by the physical sediment properties, such as porosity, but also by the interactions between benthic fauna, organic matter and microbial activity (e.g. biofilms). Furthermore, salinity gradients, hydrodynamic forces (e.g. tides, waves) and episodic events, such as storms and rainfall, also influence sediment erodibility. The influence of biological activity may also differ in muddy versus sandy sediments, where physical control (i.e. more frequent sediment transport events) may exert a stronger influence throughout the seasonal cycle (Kauppi et al. 2017) resulting in contrasting temporal

patterns of sediment erodibility among sites in different sedimentary settings. For example, the more frequent resuspension events in sandy environments may prevent the formation of a stabilizing biofilm during the warmer months in contrast to calm muddy environments. Such spatial heterogeneity is also reflected in the sediment nutrient pools and solute fluxes (Gammal et al. 2017). Sediment redox conditions and pore water nutrient concentrations may vary depending on e.g. biological activity, sediment permeability and the quantity and quality of organic matter available (Aller 1994). Consequently, the influence of sediment resuspension on nutrient fluxes may vary substantially in time and space.

Future climate scenarios predict increasing frequency of strong storms, winds and other extreme events and shortening ice winters at higher latitudes that will likely modify resuspension dynamics in coastal areas (IPCC 2013). Assessing these challenges requires understanding of resuspension dynamics and more accurate sediment transportation models. The erosion threshold is a central parameter in sediment transportation modelling and is most often estimated from median grain size (e.g. Shields 1936; Wiberg and Smith 1987; Amoudry and Souza 2011), which, however, fails to account for the natural variation in sediment erodibility associated with biota. Since the biological and physical processes are inevitably interrelated, a holistic approach is necessary when considering sediment dynamics. It is therefore important to quantify the natural variation in the erosion threshold to improve current knowledge and better parameterise sediment transport models. Previous research on sediment erodibility has tended to focus on spatial rather than temporal variability (e.g. Amos et al. 1996; Lanuru et al. 2007) and on intertidal flats (e.g. Tolhurst et al. 1999; Widdows et al. 2000; Neumeier et al. 2006) with only a few examining natural variability in subtidal sediments (Sutherland et al. 1998; Andersen et al. 2005; Grabowski et al. 2012). Furthermore, the ecological significance of resuspension on the nutrient dynamics in marine environments is poorly resolved because of contradicting results (e.g. Almroth et al. 2009; Kalnejais et al. 2010; Wengrove et al. 2015).

The main objectives of this study were to quantify spatial-temporal variation in sediment resuspension potential and associated nutrient fluxes across a sedimentary gradient and to identify environmental predictors of that variability. In a previous spatially structured study in the coastal Baltic Sea, we assessed resuspension potential across a mud-sand sedimentary gradient encompassing 18 sites (Joensuu et al. 2018), from which we selected three sites to resolve the interactions between space and time. The three sites spanned the range of sedimentary properties (median grain size 58–271 μm ; muddy, mixed and sandy sediment) and associated benthic communities sampled previously. We quantified the variation in the erosion threshold (τ_c) that marks the onset of sediment transport and is a key parameter in sediment transportation

models and the erosion constant (m_e) that describes the rate of change in sediment erosion in the later stage of the erosion process. In order to investigate the role of resuspension on nutrient dynamics, we measured pore water concentrations of ammonium (NH_4^+), phosphate (PO_4^{3-}) and dissolved silicate ($\text{Si}(\text{OH})_4$) to quantify the potential sediment nutrient pool, and the change (%) in these nutrient concentrations in the near bottom water after the erosion threshold was exceeded. In the Baltic Sea eutrophication is a serious problem and our focus on these nutrients reflects their importance to primary producers and because they are also monitored to evaluate the nutrient status.

Methods

Study Sites

The study area is located on the north-west coast of the Gulf of Finland in the Baltic Sea (Fig. 1) where the weather conditions are dominated by the humid continental climate with warm summers and cold winters. The period of ice cover varies annually from 0 to 4 months, but the sea was not frozen during the sampling period. The study area is non-tidal and hydrodynamics are dominated by wind-driven waves and large-scale currents, such as upwelling events, which can initiate sediment resuspension events (Haapala 1994; Lehmann and Myrberg 2008; Valanko et al. 2010). Based on a previous study focused on spatial variations in sediment resuspension potential from the same area (Joensuu et al. 2018), we selected

three sites to quantify temporal variability in sediment erodibility and resuspension related nutrient fluxes (Fig. 1). Site I ($59^\circ 50.749$ N, $23^\circ 14.897$ E, water depth = 2.3 m) is characterized by a high mud and organic content and low macrofaunal abundance and species richness (Table 1). Sites II ($59^\circ 50.480$ N, $23^\circ 14.637$ E, 3.0 m) and III ($59^\circ 50.487$ N, $23^\circ 14.984$ E, 3.4 m) are moderately sheltered sandy sites with lower organic content, but higher macrofaunal abundance and species richness. These three sites span the range of sedimentary environments in the study area (Joensuu et al. 2018). The most abundant macrofaunal species in the study area were bivalve *Macoma balthica* and gastropoda *Hydrobiidae* (Table 1). Sites I and II were sampled every second month and the site III every month from April to December 2015 (see Table 2 for exact dates). Site III was sampled more frequently to monitor shorter-term changes in environmental conditions.

Field Sampling

At each site, a 5×5 m plot was marked for resampling over subsequent months. The sampling area was chosen to be as homogenous as possible (e.g. vegetated patches were avoided) to minimize the influence of a small-scale variation within the local habitat. Within plot sampling locations were recorded in order not to re-sample them on subsequent visits. Temporal variability in resuspension potential metrics and related nutrient fluxes were investigated with core-based erosion device (EROMES, described below). At each sampling time/site, four EROMES cores (diameter 10 cm) were carefully placed and pushed 10 cm deep into the sediment. Three

Fig. 1 Location of sampling sites in the Hanko archipelago, Baltic Sea

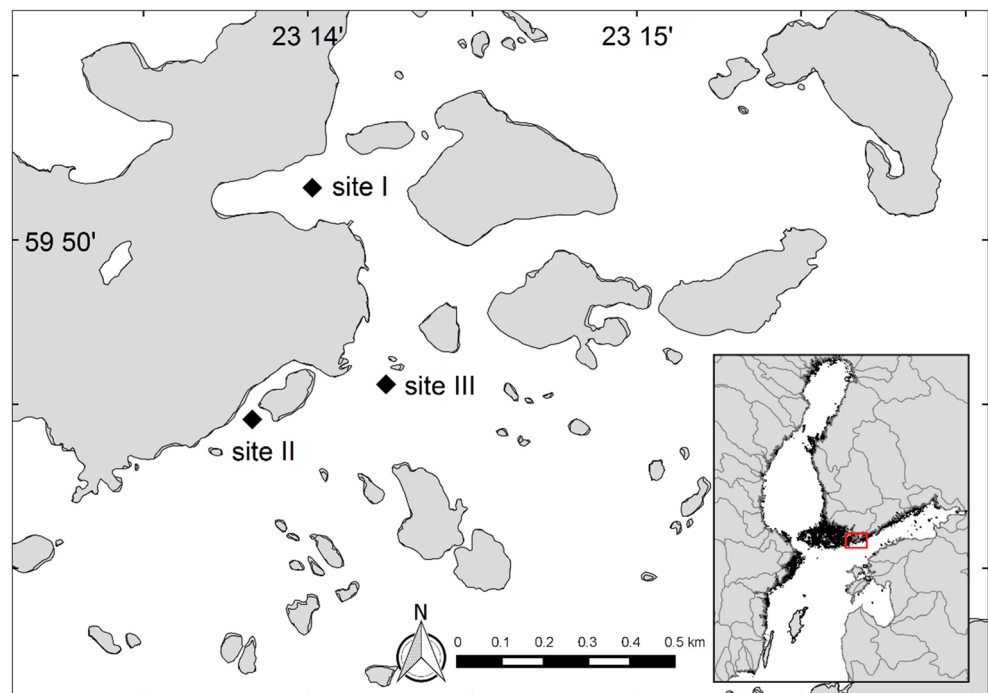


Table 1 Seasonal summary of environmental variables (mean and range (min–max)) at each site. See Online Resource 1 for temporarily resolved data

	Site I (n = 18)	Site II (n = 20)	Site III (n = 35)
Sediment properties			
Median particle size (μm)	58 (23–69)	175 (134–281)	271 (252–285)
Clay ($\leq 2 \mu\text{m}$) content (%)	8.1 (5.9–13.0)	1.3 (0.7–3.6)	0.3 (0.1–0.7)
Mud ($< 63 \mu\text{m}$) content (%)	48.5 (35.2–77.8)	7.9 (4.0–21.5)	1.6 (0.8–4.0)
Dry bulk density (g cm^{-3})	1.4 (1.4–1.5)	1.8 (1.6–2.0)	1.9 (1.9–2.0)
Water content (%)	50.4 (45.6–57.6)	26.5 (20.4–39.3)	22.9 (20.3–26.0)
Porosity	0.5 (0.5–0.6)	0.3 (0.2–0.4)	0.2 (0.2–0.3)
Organic content (%)	3.6 (2.6–4.7)	1.2 (0.5–3.1)	0.7 (0.5–1.0)
Microalgal biomass ($\mu\text{g g}^{-1}$)			
Chlorophyll <i>a</i>	18.8 (14.2–26.7)	21.4 (12.3–37.5)	26.5 (17.6–38.2)
Phaeopigment	15.4 (12.4–20.1)	7.2 (2.7–20.3)	4.5 (0.0–10.0)
Extracellular polymeric substances	325 (83–531)	30 (10–67)	396 (0–848)
Macrofauna			
Species richness (ind. core $^{-1}$)	4 (2–6)	6 (4–8)	6 (1–8)
Biomass (g core^{-1})	0.2 (0.0–0.6)	0.7 (0.1–2.0)	0.7 (0.1–1.8)
Abundance (ind. core $^{-1}$)	19 (5–56)	46 (15–92)	42 (2–105)
<i>Hydrobiidae</i>	8 (1–21)	26 (8–68)	22 (2–56)
<i>Macoma balthica</i>	10 (2–38)	12 (4–30)	6 (0–20)
<i>Hediste diversicolor</i>	1 (0–4)	3 (0–7)	2 (0–7)
<i>Marenzelleria</i> sp.	0 (0–1)	2 (0–5)	6 (0–24)
<i>Oligochaeta</i>	0 (0–1)	2 (0–7)	4 (0–16)

Table 2 Seasonal variations in temperature (Temp), salinity (Sal) and oxygen (O_2) concentrations at the sea bed and nutrient concentrations in the near bottom water (NBW) before EROMES experiments and in pore water (PW) at 1 and 3 cm depth for each site

Site	Date	Temp ($^{\circ}\text{C}$)	Sal	O_2 (mg L^{-1})	NH_4^+ ($\mu\text{mol L}^{-1}$)			PO_4^{3-} ($\mu\text{mol L}^{-1}$)			$\text{Si}(\text{OH})_4$ ($\mu\text{mol L}^{-1}$)		
					NBW	PW 1 cm	PW 3 cm	NBW	PW 1 cm	PW 3 cm	NBW	PW 1 cm	PW 3 cm
I	29.4.2015	6.0	5.3	11.9	0.9	3.1	15.0	0.2	9.8	15.0	4.9	23.9	34.5
	25.6.2015	–	–	–	1.3	9.9	69.3	0.3	32.6	74.6	20.3	10.9	86.5
	27.8.2015	18.8	5.4	9.9	1.7	30.7	117.8	0.2	66.9	58.3	7.9	21.8	258.4
	15.10.2015	10.7	5.6	10.6	1.5	82.2	137.7	0.2	36.9	33.4	13.1	222.0	211.3
	15.12.2015	5.3	5.9	11.6	2.0	48.9	86.3	0.7	15.2	25.3	20.5	72.9	202.1
II	27.4.2015	5.0	5.7	–	1.5	2.0	8.0	0.2	0.5	2.2	2.1	6.3	10.5
	24.6.2015	12.7	5.9	11.3	2.0	4.2	3.4	0.2	0.6	6.3	–	5.2	18.1
	26.8.2015	19.1	5.3	9.9	1.2	9.7	15.4	0.2	7.1	7.9	8.4	12.7	20.9
	13.10.2015	10.1	5.6	11.7	0.3	11.7	21.3	0.3	1.0	3.3	–	–	12.7
	14.12.2015	5.5	6.0	11.5	2.4	18.8	28.4	0.6	6.3	3.6	5.5	44.7	62.9
III	28.4.2015	4.6	5.7	12.2	1.0	2.3	6.3	0.2	0.2	0.4	4.2	2.8	4.2
	2.6.2015	10.0	5.6	10.5	1.0	7.5	17.9	0.2	0.6	2.8	1.6	3.9	7.8
	23.6.2015	14.5	5.7	11.5	1.2	0.2	2.7	0.2	0.4	0.9	6.9	4.5	5.1
	28.7.2015	13.0	5.9	10.5	0.7	16.5	29.1	0.2	0.9	4.4	0.0	4.7	9.6
	25.8.2015	19.8	5.4	10.7	2.2	0.5	1.2	0.1	0.6	0.8	7.7	4.1	3.3
	30.9.2015	–	–	–	1.1	1.2	5.5	0.3	0.7	1.5	15.0	7.1	8.5
	14.10.2015	9.8	5.7	10.8	2.3	16.6	31.2	0.3	1.9	2.4	15.4	7.4	19.9
	3.11.2015	9.5	5.8	10.8	6.9	12.1	23.2	0.4	0.3	0.8	16.8	5.2	6.2
16.12.2015	5.3	6.0	11.7	3.3	10.5	28.1	0.7	1.0	3.7	19.4	17.4	27.6	

surface samples were taken with three 100 mL syringes (diameter 3.5 cm) from 0 to 0.5 cm depth next to each EROMES core before its removal. The three sediment surface samples for each EROMES core were pooled, homogenized and divided into two subsamples. In addition, one sediment core (diameter 8 cm, 15 cm depth) was collected for the analysis of grain size distribution and pore water nutrient concentrations. The sediment core had 2 mm holes every 1 to 5 cm depth (taped during the collection from the seabed) to enable pore water sampling with rhizon samplers (diameter 2.5 mm, pore size 0.15 μm). The rhizon samplers were carefully pushed through the holes and into the sediment immediately after the collection and pore water was withdrawn with vacuum syringes. The EROMES cores and sediment surface samples were kept in a water bath at in situ temperatures and transported back to the laboratory (15 min). Since it was not possible to analyse sediment characteristics or pore water nutrient concentrations directly after the collection, both were frozen to extend the preservation time until analysed. In addition, water temperature, salinity and oxygen concentration at the bottom were measured in situ each time/site with the Citadel CTD-NV (Teledyne RD Instruments) and near bottom water was collected with a hose to a canister for further use and kept in situ temperature.

Sediment Resuspension Potential Measurements

Resuspension potential metrics of erosion threshold and erosion constant were determined with a portable EROMES device (Schünemann and Kühl 1991). Prior to the measurements, water level in the EROMES cores were gently adjusted to 20 cm above the sediment surface by removing excess water. A propeller was positioned 3 cm and an OBS-sensor 6.5 cm above the sediment surface to generate shear stress on the sediment surface and monitor turbidity. To prevent rotational flow in the cores, a baffle ring was positioned 1.5 cm above the sediment. A previously published EROMES calibration involving quartz sand with known critical shear stresses was used to convert the propeller revolutions to a nominal bed shear stresses (Schünemann and Kühl 1991; Andersen 2001). The bed shear stress was set to increase every 2 min by 0.1 N m^{-2} from 0 to 1.6 N m^{-2} . The OBS-sensor was calibrated to suspended solids concentration (SSC; mg L^{-1}) from water samples taken with a 100-mL syringe from the cores during the erosion measurements (Andersen 2001; Andersen and Pejrup 2002). The removed water was immediately replaced with 100 mL of near bottom water from the site.

Separate OBS-SSC calibrations were made for each site and sampling time ($r^2 = 0.83\text{--}0.99$, $n = 12\text{--}16$), and erosion rate was then derived from the time derivative of the SSC concentration with increasing bed shear stress. The erosion rate was plotted against nominal bed shear stress to determine the erosion threshold (τ_c ; N m^{-2}) and the erosion constant (m_e ;

$\text{g N}^{-1} \text{s}^{-1}$). τ_c was defined as the bed shear stress sufficient to produce the erosion rate of 0.1 $\text{g m}^{-2} \text{s}^{-1}$ and describes the initial erosion of the bed after the resuspension of unconsolidated ‘fluffy’ material (Andersen 2001; Andersen et al. 2005). If 0.1 $\text{g m}^{-2} \text{s}^{-1}$ was not exceeded during an EROMES run, τ_c was estimated by extrapolation of the linear relationship between the erosion rate and the bed shear stress. The erosion constant (m_e ; $\text{g N}^{-1} \text{s}^{-1}$) is defined as the change in the erosion rate as a function of bed shear stress between 1.0–1.6 N m^{-2} and describes the later stage of the erosion process following the exceedance of τ_c (Harris et al. 2015). High values of τ_c indicate more stable sediment as more energy is needed to initiate the particle motion where high values of m_e indicate rapid erosion of the sub-surface layer of the sediment after the surface layer has been eroded.

Nutrient Analyses

To determine nutrient release from the sediments during the resuspension potential measurements, the change in the near bottom water nutrient concentrations of dissolved ammonium (NH_4^+), phosphate (PO_4^{3-}) and dissolved silicate ($\text{Si}(\text{OH})_4$) were analysed from water samples at fixed shear stress steps based on a priori knowledge of the expected erosion thresholds from the area (Joensuu et al. 2018). The expected erosion thresholds were 0.39–0.76 N m^{-2} for site I, 0.61–0.93 N m^{-2} for site II and 0.79–1.02 N m^{-2} for site III. Accordingly, nutrient concentrations were measured at following steps for each Site; Site I 0.2, 0.6, 0.8, 1.5 N m^{-2} , site II 0.2, 0.8, 1.0, 1.5 N m^{-2} and site III 0.2, 0.8, 1.1, 1.5 N m^{-2} as well as at the start and end of each erosion run. Water samples collected for the SSC analyses were also used for the nutrient analyses. The water samples were filtered immediately after the collection through 0.2 μm sterile filters and frozen prior to analyses with standard photometric methods (Lachat QuickChem 8000) together with the pore water nutrient samples. All equipment used for nutrient sampling were carefully acid washed and rinsed with purified MQ-water prior to use. The nutrient concentration in the step following exceedance of τ_c , C_n ($\mu\text{mol L}^{-1}$) (which varied with site and time) was used to calculate the change (as a percentage) in the near bottom water concentration measured at the start of the EROMES run (C_{nbw}) as follows (after correcting for dilution caused by water replacement after sampling):

$$(\%) \text{ change} = \frac{(C_n - C_{nbw})}{C_n} \times 100$$

Based on the measured erosion thresholds, the C_n shear stress were as follows: site I 0.6 N m^{-2} (April, June and December), 0.8 N m^{-2} (August) and 1.5 N m^{-2} (October); site II 1.5 N m^{-2} (April, August and October) and 1.1 N m^{-2} (June and December); and site II 1.6 N m^{-2} (April, June¹, July,

August and September) and 1.5 N m^{-2} (October and November) at site III. A positive (%) change in the near bottom water nutrient concentrations implies release from the sediment and whereas a negative value indicates no release and higher nutrient concentrations in the near bottom water.

Environmental Variables

We quantified abiotic (dry bulk density, water and organic content, and grain size distribution) and biotic (species richness, macrofaunal abundance and biomass, and concentrations of chlorophyll *a*, phaeopigment and extracellular polymeric substances (EPS)) variables at each sampling time (Online Resource 1). Concentrations of chlorophyll *a*, phaeopigment and colloidal carbohydrate fraction (a proxy for EPS) were analysed from a lyophilized subsample. Samples for chlorophyll *a* and phaeopigment concentration measurements were treated with acetone and left in darkness for 24 h at 4 °C and then centrifuged at 3000 rpm (10 min 20 °C). The absorbance of the supernatant was measured spectrophotometrically at 665 and 750 nm wavelengths before and after acidification and calculations followed Lorenzen (1967). The phenol-sulphuric acid assay (Dubois et al. 1956; Underwood et al. 1995) was used to estimate the colloidal (soluble) carbohydrate fraction (results in glucose equivalents). Both pigments and colloidal carbohydrate fraction were standardized to sediment dry weight ($\mu\text{g g}^{-1}$). Fresh subsamples were used for analyses of water and organic content (%) and dry bulk density (g cm^{-3}). The sediment-water content and dry bulk density were determined after drying (105 °C for 12 h) and organic content by loss-on-ignition (450 °C for 4 h). Calculations followed Tolhurst et al. (2006) for water content and Roberts et al. (1998) for dry bulk density. For the estimation of dry bulk density, a sediment particle density of 2.65 g cm^{-3} (Mehta and Lee 1994; Avnimelech et al. 2001) and water density of 1.0 g cm^{-3} were used. Grain size distribution was analysed from the sediment core after removing large shell fragments. Sediment was treated with hydrogen peroxide (H_2O_2 , 6%) to dissolve the organic material; sieved with 63, 250 and 500 μm mesh; and finally the percent of each size fractions were measured. The median particle size (μm) and mud ($< 63 \mu\text{m}$) and clay ($\leq 2 \mu\text{m}$) content (%) were analysed with a GRADISTAT program (Blott and Pye 2001). Benthic macrofauna were extracted from the EROMES cores at the end of each run by sieving the sediment on a 500- μm mesh. The macrofauna were stored in 70% ethanol, stained (Rose Bengal) and identified to the lowest taxonomic level practical (usually species).

Statistical Analyses

A pair-wise PERMANOVA test (based on 9999 permutations) was used to investigate differences in resuspension potential metrics between sites. All three sites differed ($p = 0.001$) and therefore they were analysed separately. Distance-based linear modelling (DistLM) was used to identify environmental predictors of resuspension potential metrics and how much of this variation they could explain. Separate Euclidean distance resemblance matrixes were computed for each resuspension measures (τ_c , m_e) with permutation techniques. Marginal tests (9999 permutations) were used to identify individual predictors correlated (p value ≤ 0.1) with the resuspension potential measures and then a step-wise selection procedure used to find the combination of these variables that explained the greatest amount of variation. Model selection was based on a corrected Akaike's information criterion (AICc) and highly correlated (Pearson's $r > 0.8$) environmental variables were excluded from the analyses (Online Resource 2). Environmental variables were transformed (square root, fourth root and logarithmic), if necessary, and normalized before the DistLM analysis. The PERMANOVA and DistLM analyses were carried out with the PRIMER 7 PERMANOVA+ (Clarke and Gorley 2015). The coefficient of variation (CV = standard deviation / mean) was used to compare the magnitude of the variation in environmental variables and resuspension potential metrics independently from the measurement unit.

Results

Temporal Variation in Resuspension Potential Metrics

The muddy site I exhibited a clear temporal pattern in resuspension potential metrics, whereas the mixed site II showed some and the sandy site III negligible variation (Fig. 2). The magnitude of the temporal variation in τ_c at site I was twice as high than at site II and three times higher than at site III (Table 3). At site I, the lowest τ_c values were observed in the cooler months of April and December and were four times lower than the highest values in October (Fig. 2a). Correspondingly, the highest m_e values were found in April and lowest in October, but interestingly the m_e also remained low in December despite the low τ_c values (Fig. 2d). At site II, the τ_c values were two times higher in April compared to the lowest values in early June and December (Fig. 2b). The temporal variation in m_e was similar to that observed in τ_c ; the m_e values were lowest in April and highest in early June and December (Fig. 2f). The τ_c values at the site III were lowest in April and December and 1.2–1.3 times higher in early and late June and in November (Fig. 2c). Correspondingly, m_e values were highest in April and December but remained generally very low in other months (Fig. 2g).

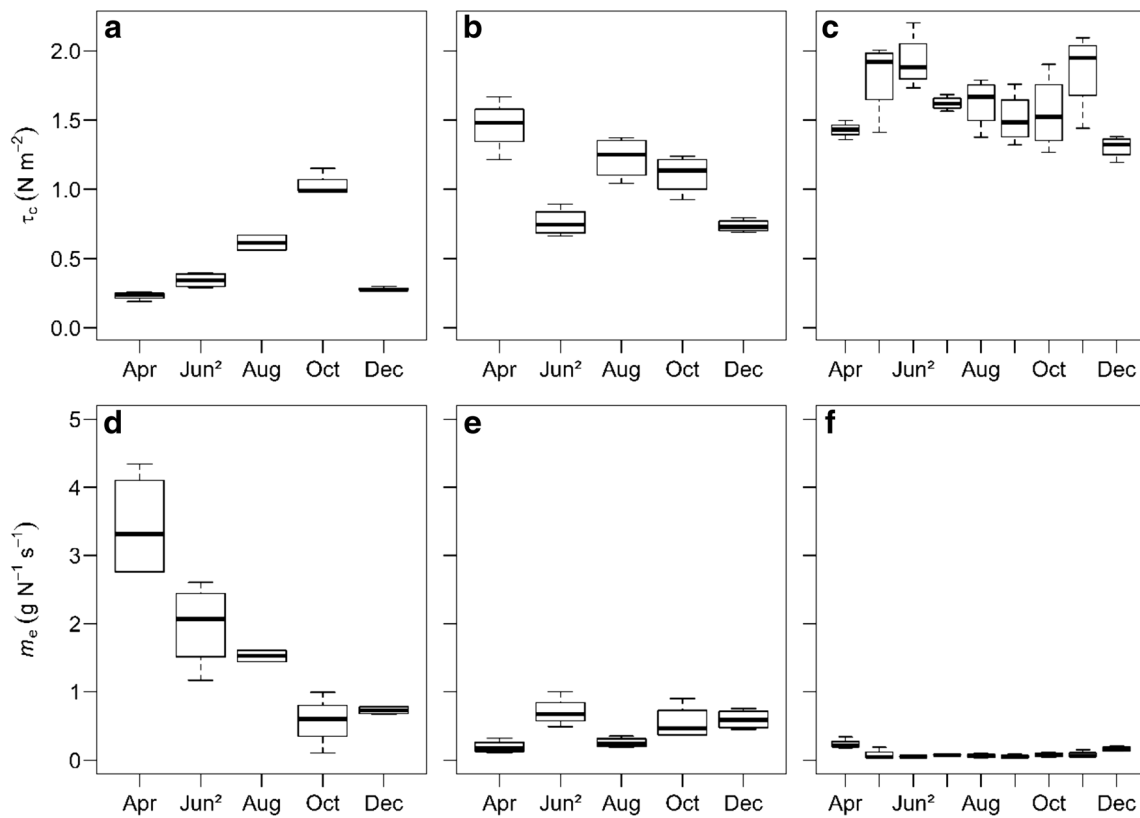


Fig. 2 Temporal variation in the erosion threshold (τ_c) and erosion constant (m_e) at sites I (a, d), II (b, e) and III (c, f). Boxes represent 25%, median and 75% distributions, with whiskers the non-outlier minimum and maximum. The n is 4 per month, except in August at site I ($n=2$) and in April at site III ($n=3$)

Table 3 Coefficient of variations for the environmental variables and resuspension potential measures (τ_c , erosion threshold; m_e , erosion constant) as a function of site

	Site I ($n=18$)	Site II ($n=20$)	Site III ($n=35$)
Sediment properties			
Median particle size (μm)	24	21	2.8
Mud content (%)	23	59	35
Dry bulk density (g cm^{-3})	33	5.6	1.5
Water content (cm^{-3})	6.2	19	5.6
Organic content (g)	16	56	18
Microalgal biomass ($\mu\text{g g}^{-1}$)			
Chlorophyll <i>a</i>	18	32	19
Phaeopigment	15	66	54
EPS	43	56	69
Macrofauna			
Species richness (ind. core ⁻¹)	35	21	23
Biomass (g core ⁻¹)	98	66	67
Abundance (ind. core ⁻¹)	70	42	46
<i>Hydrobiidae</i>	73	57	58
<i>Macoma balthica</i>	108	60	62
Resuspension potential			
τ_c (N m^{-2})	67	29	16
m_e ($\text{g N}^{-1} \text{s}^{-1}$)	73	55	70

At site I, τ_c increased with increasing dry bulk density ($p = 0.03$, $n = 18$) (Table 4 and Fig. 3a). Since the dry bulk density is inversely correlated with the water content, low values in the dry bulk density indicate high water content and a porous surface sediment that is easily eroded. The low τ_c values and high m_e values in April demonstrate that the sediment was easily eroded, and the erosion rate increased quickly with increasing shear stress compared to the other months (Fig. 2a, d). The water and organic content and microbial biomass were higher at this time (Online Resource 1a). The m_e increased with increasing abundance of *M. balthica* ($p = 0.004$, $n = 18$) suggesting that this species may destabilize the sediment (Table 4 and Fig. 3b). The DistLM analysis identified the best combination of environmental variables explaining most of the temporal variation in the resuspension potential metrics. For τ_c , that combination included the dry bulk density and the abundance of *Hydrobiidae*, which together explained 44% of the total variation in τ_c (Table 5). Macrofaunal variables (the abundance of *M. balthica* and species richness) explained a large proportion of the variance in m_e (73%) and together with organic content explained 81% in total (Table 5).

Dry bulk density was also the best predictor for τ_c at the sites II and III and also for m_e at site II (Tables 4 and 5). Curiously, however, the direction of the correlation at site II was opposite to that observed at sites I and III (compare Fig. 3c with Fig. 3a, e). In addition, the magnitude of the temporal variation in dry bulk density was markedly higher at site II

(CV = 5.6%) compared to sites I (2.7%) and III (1.5%) (Table 3). At site II, the lowest values in the dry bulk density were found in April (1.6 g cm^{-3}) when measures of microbial biomass peaked (Online Resource 1b). The τ_c increased and m_e decreased with the chlorophyll *a* ($p = 0.004$ and 0.03 , respectively, $n = 20$) and phaeopigment concentration ($p = 0.006$ and 0.1 , respectively, $n = 20$), and the abundance of *M. balthica* ($p = 0.01$ and 0.06 , respectively, $n = 20$) suggesting that biota may seasonally alter the sediment dry bulk density, i.e. water content, at site II (Fig. 3d, Table 4). At site III, a combination of chlorophyll *a* concentration and the dry bulk density were the best predictors of m_e , explaining in total 18% of the variation (Fig. 3f, Table 5). Overall, the amount of variation in m_e explained environmental variables decreased from site I (81%) to sites II (31%) and III (18%) but no such pattern was seen for τ_c where the amount of variation explained ranged from 38% (site III) to 46% (site II).

Nutrient Dynamics

Sediment Pore Water Nutrients

In general, sediments were potential nutrient sources at all sites, but especially at muddy site I (Table 2). The pore water nutrient concentrations were generally higher in the surface layer of muddy sediments in comparison to more permeable sandy sediments. Overall, the temporal variation in sediment

Table 4 Proportion of variation (prop.) in resuspension potential metrics (τ_c , erosion threshold; m_e , erosion constant) explained by environmental variables (marginal DistLM results)

		Variable	Pseudo- <i>F</i>	Prop.		
Site I ($n = 18$)	τ_c	Dry bulk density (g cm^{-3})	5.55	0.26	**	(+)
		Species richness	4.19	0.21	**	(+)
		Phaeopigment ($\mu\text{g g}^{-1}$)	3.25	0.17	*	(-)
	m_e	<i>Macoma balthica</i> (ind. core ⁻¹)	13.31	0.45	***	(+)
		Phaeopigment ($\mu\text{g g}^{-1}$)	8.81	0.36	***	(+)
		Organic content (%)	7.03	0.31	**	(+)
		Species richness	2.93	0.15	*	(-)
Site II ($n = 20$)	τ_c	Dry bulk density (g cm^{-3})	15.17	0.46	***	(-)
		Phaeopigment ($\mu\text{g g}^{-1}$)	10.72	0.37	***	(+)
		Chlorophyll <i>a</i> ($\mu\text{g g}^{-1}$)	9.10	0.34	***	(+)
		<i>Macoma balthica</i> (ind. core ⁻¹)	7.97	0.31	***	(+)
	m_e	Dry bulk density (g cm^{-3})	7.97	0.31	***	(+)
		Chlorophyll <i>a</i> ($\mu\text{g g}^{-1}$)	5.51	0.23	**	(-)
		<i>Macoma balthica</i> (ind. core ⁻¹)	3.92	0.18	*	(-)
Site III ($n = 35$)	τ_c	Phaeopigment ($\mu\text{g g}^{-1}$)	2.41	0.12	*	(-)
		Dry bulk density (g cm^{-3})	20.30	0.38	***	(+)
	m_e	Chlorophyll <i>a</i> ($\mu\text{g g}^{-1}$)	3.38	0.10	*	(+)
		Dry bulk density (g cm^{-3})	3.28	0.09	*	(-)
		<i>Hydrobiidae</i> (ind. core ⁻¹)	2.94	0.08	*	(+)

Levels of statistical support are *weak ($p \leq 0.1$), **moderate ($p \leq 0.05$) and ***strong ($p \leq 0.01$); the direction of the correlation is given in parentheses

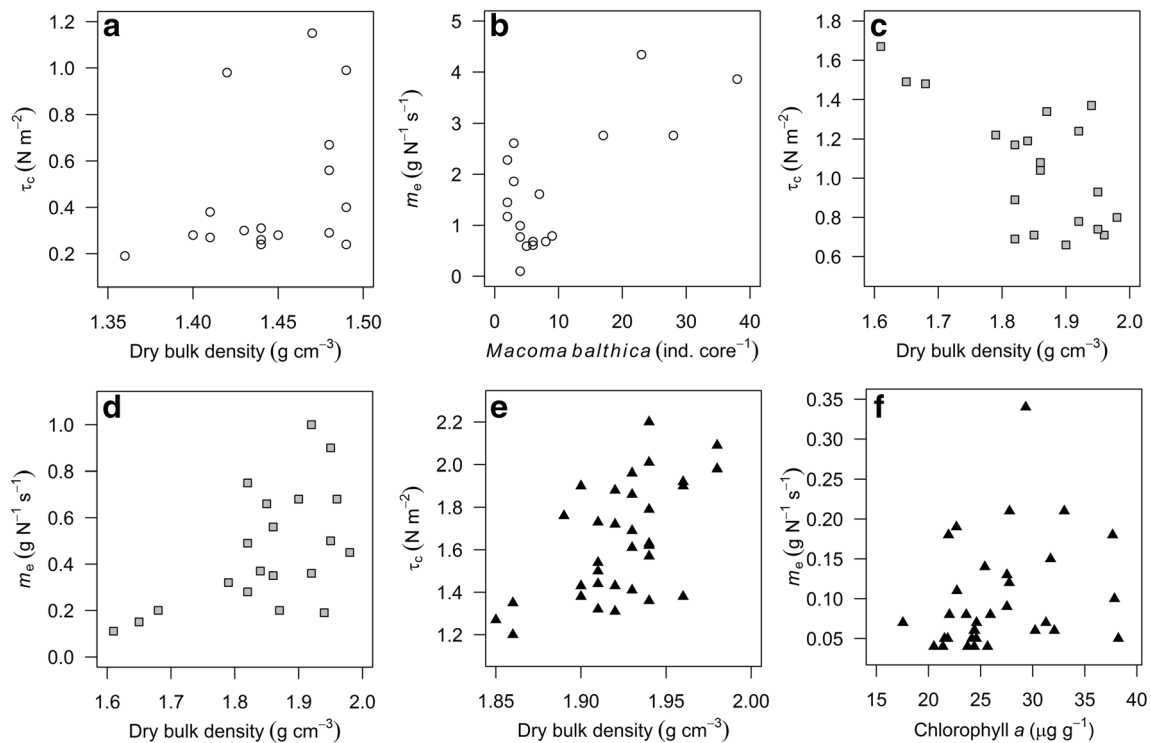


Fig. 3 The best single predictors of erosion threshold (τ_c) and erosion constant (m_e) at sites I (a, b), II (c, d) and III (e, f). See Table 4 for a full list of predictors and statistical relationships

pore water nutrient concentrations was fivefold greater at site I compared to site II and 5–20 times greater than site III (Table 2). The pore water concentration of NH_4^+ in the surface layer of the sediment (0–1 cm) ranged between 3.1–82 $\mu\text{mol L}^{-1}$ at site I, 2.0–19 $\mu\text{mol L}^{-1}$ at site II and 0.2–17 $\mu\text{mol L}^{-1}$ at site III. The pore water concentrations of NH_4^+ were highest in October at sites I and III and in December at site II and lowest in April at sites I and II and in late June at site III. Surprisingly, the temporal variation in organic content was not correlated with the pore water nutrient concentrations (Table 2 and Online Resource 1).

Interestingly, at site III the pore water concentrations of NH_4^+ in the sediment surface layer were lower in late June

(0.2 $\mu\text{mol L}^{-1}$) and August (0.5 $\mu\text{mol L}^{-1}$) than the near bottom water concentrations (1.2 and 2.2 $\mu\text{mol L}^{-1}$, respectively) (Table 2) suggesting either potential resuspension events and associated nutrient release at these times or advective transport of nutrients from other sources. The sediment pore water concentrations of PO_4^{3-} were substantially higher at site I (9.8–67 $\mu\text{mol L}^{-1}$) in contrast to sites II (0.5–7.1 $\mu\text{mol L}^{-1}$) and III (0.2–1.9 $\mu\text{mol L}^{-1}$). Pore water PO_4^{3-} concentrations in the sediment surface layer were highest in August at sites I and II and in October at site III and lowest in April at all sites. $\text{Si}(\text{OH})_4$ pore water concentrations exhibited the highest temporal variation at all sites ranging between 11–222 $\mu\text{mol L}^{-1}$ at site I, 5.2–45 $\mu\text{mol L}^{-1}$ at site II and 2.8–17 $\mu\text{mol L}^{-1}$ at site

Table 5 The environmental variables best explaining temporal variation in resuspension potential metrics (τ_c , erosion threshold; m_e , erosion constant) based on the step-wise sequential test and corrected Akaike information criterion (AICc). The proportion of variation (prop.) explained by each environmental variable and cumulatively (cum.) are shown

		Variable	AICc	Prop.	Cum.	
Site I (n = 18)	τ_c	Dry bulk density (g cm^{-3})	-32.82	0.26	0.26	**
		<i>Hydrobiidae</i> (ind. core ⁻¹)	-35.12	0.19	0.44	**
	m_e	<i>Macoma balthica</i> (ind. core ⁻¹)	-0.41	0.45	0.45	***
		Species richness	-10.10	0.27	0.73	***
		Organic content (%)	-13.47	0.08	0.81	**
Site II (n = 20)	τ_c	Dry bulk density (g cm^{-3})	-55.38	0.46	0.46	***
	m_e	Dry bulk density (g cm^{-3})	-58.35	0.31	0.31	***
Site III (n = 35)	τ_c	Dry bulk density (g cm^{-3})	-106.9	0.38	0.38	***
	m_e	Chlorophyll a ($\mu\text{g g}^{-1}$)	-183.06	0.10	0.10	*
		Dry bulk density (g cm^{-3})	-184.04	0.09	0.18	*

Levels of statistical support are *weak ($p \leq 0.1$), **moderate ($p \leq 0.05$) and ***strong ($p \leq 0.01$)

III. The pore water concentration of $\text{Si}(\text{OH})_4$ was highest in October at site I and in December at sites II and III. The lowest values were observed in late June at all sites. It is notable, however, that the near bottom water concentration of $\text{Si}(\text{OH})_4$ at site III was mostly greater than that observed in surface (0–1 cm) sediment pore water (Table 2).

Sediment Resuspension and Nutrient Fluxes

During EROMES measurements, τ_c was exceeded (i.e. an erosion rate $> 0.1 \text{ g m}^{-2} \text{ s}^{-1}$) in 17 out of 18 runs at site I, 19 of 20 runs at site II and 16 of 35 runs at site III. Runs where τ_c was not exceeded were excluded from estimates of sediment resuspension-driven nutrient fluxes. Quantitative comparisons between pore water nutrient concentrations and nutrient concentrations in the EROMES cores after sediment resuspension were not relevant, because the pore water samples were measured at 1 cm depth intervals compared to a few millimetres of sediment erosion in the EROMES cores.

Interestingly, the impact of sediment resuspension on water column nutrient concentrations was at the same level or lower at site I compared to sites II and III, despite higher sediment pore water concentrations and lower erosion thresholds at these sites (Table 2, Fig. 4). Overall, sediment resuspension influenced near bottom water nutrient concentrations at sites I and II, but not markedly at site III (Fig. 4, Online Resource 3). Sediment resuspension increased the nutrient concentration of NH_4^+ in the near bottom water between 20 and 90% on average at sites I and II, respectively (Online Resource 3). The highest changes were observed in April and August at site I (Fig. 4a) and in April and October at site II (Fig. 4b). The impact of sediment resuspension on water column PO_4^{3-} concentration was generally very small at all sites, most likely because the near bottom water and sediment surface remained oxic all year round (Fig. 4, Table 2). The greatest increase was observed at site I where resuspension increased the PO_4^{3-} concentration by $\sim 10\%$ (Online Resource 3) with the highest positive change occurring in August when the surface sediment pore water concentration was highest (Fig. 4d, Table 2). Following sediment resuspension the concentration of $\text{Si}(\text{OH})_4$ increased on average by 30 and 180% at sites I and II, respectively (Online Resource 3). At site I, sediment resuspension increased the $\text{Si}(\text{OH})_4$ concentration by a similar amount each month (Fig. 4g), while at site II, the highest changes were observed in April and December (Fig. 4h).

Discussion

The purpose of this study was to determine how temporal variations in environmental (abiotic and biotic) conditions influenced sediment erodibility and resuspension-associated nutrient fluxes in subtidal coastal sediments. Our study included

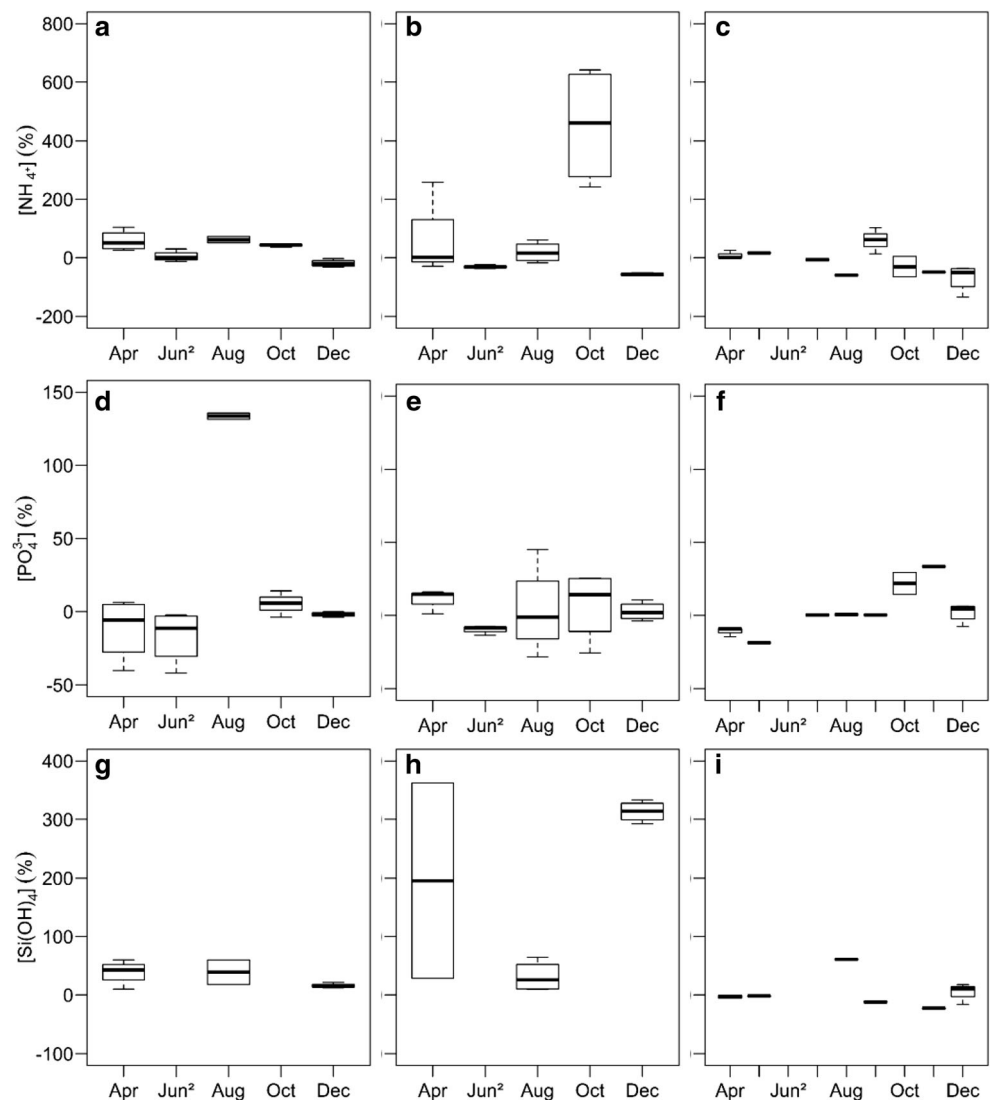
three sampling sites encompassing muddy, mixed and sandy sediments, which were sampled regularly from April to December. Sediment erosion and resuspension in these shallow sites is dominated by wind-waves, which create turbulent fluctuations and shear stress at the sediment surface. The EROMES device used to measure resuspension potential creates similar turbulent fluctuations at the sediment surface (Lanuru et al. 2007; Widdows et al. 2007), mimicking those generated by wave motion. Overall, the muddy sediment (site I) showed a clear temporal pattern in resuspension potential metrics in contrast to the mixed (site II) and sandy sediments (site III), where temporal variation was less distinct, and potentially governed more by the dynamic nature of those environments.

Temporal variation in environmental variables were measured in situ and correlated with the erodibility of natural sediments. The dry bulk density (equal to water content of the sediment) was found to be the best predictor of sediment erodibility at all sites. The temporal variation in the dry bulk density was generally low, yet clearly important for the initiation of sediment transport (Table 3). In addition, the seasonal dynamics of benthic macrofauna impacted on the erodibility of the muddy sediment likely by altering the dry bulk density. The biota occasionally played a role also in the mixed sediment with sedimentary chlorophyll *a* concentration and macrofauna correlated with the resuspension potential. Sediment resuspension increased nutrient concentrations in the near bottom water in muddy and mixed sediments, where occasional resuspension events may supply small amounts of nutrients to the overlaying water. Such effects were negligible in sandy sediments, where pore water nutrient concentrations were overall smaller in the surface layers of the sediment.

Temporal Variation in Sediment Erodibility

The overall results show a gradual shift from the sheltered muddy bottom, where a clear temporal pattern in sediment erodibility was observed, to the more dynamic and exposed sandy bottoms with some or negligible temporal variation. With respect to the sediment properties, the differences in erodibility of natural sediments often results from the differences in bulk density, water content and porosity (Roberts et al. 1998; Grabowski et al. 2011), which was also seen in this study. Despite limited temporal variability in dry bulk density, it was overall the best predictor for sediment erodibility, highlighting the importance of even small changes in sediment consolidation. Indeed, even though the importance of clay and silt content for the erodibility of muddy sediment is well acknowledged in the literature (e.g. Winterwerp and van Kesteren 2004), our results suggest that temporal variation in the erodibility of this type of sediment results from the changes in the dry bulk density (or water content), regardless of the cohesiveness of the sediment. The fraction of very fine sediments varied temporally between 6 and 13%

Fig. 4 The percentage change in NH_4^+ , PO_4^{3-} and $\text{Si}(\text{OH})_4$ concentrations in the water overlying the sediment in EROMES cores following exceedance of the erosion threshold at sites I (a, d, g), II (b, e, h) and III (c, f, i). A positive value indicates nutrient flux from the sediment, whereas negative flux indicates higher concentration in the overlying water. The boxes represent 25%, median and 75% distributions, with whiskers the non-outlier minimum and maximum ($n = 1\text{--}4$ per month)



(clay) and 35–78% (mud) meaning that cohesive forces were continuously present and could not explain the temporal variation in τ_c at site I (muddy sediment). This was further supported by the fact that the highest fractions of mud and clay were observed in October (52.2 and 8.7%, respectively) and December (55.9 and 9.3%, respectively), which represented opposite ends of τ_c (1.04 and 0.28 N m^{-2} , respectively) at site I.

In the DistLM analysis, the dry bulk density and abundance of *Hydrobiidae* were found to explain most of the temporal variation in τ_c at site I. The τ_c decreased at site I when sediment became less consolidated, i.e. the dry bulk density decreased. The seasonal phytoplankton growth in the study area begins with a spring bloom in March, which results in sedimentation of organic matter to the seafloor (Heiskanen and Leppänen 1995). The high organic content and photosynthetic pigment biomass in April at site I suggest sedimentation of the spring bloom, which resulted in high microbial activity and formation of a visible biofilm on the sediment surface (pers.

obs.). However, high water content at the time of sampling indicates that the sediment surface remained loosely consolidated and easily erodible despite the biofilm (Online Resource 1a). Similar to our results, Maa and Kim (2002), Dickhudt et al. (2009) and Xu et al. (2014) also found more erodible sediment in spring when freshly deposited material existed on the sediment surface. In addition, the abundance of bivalve *M. balthica* was higher in April compared to other months and could explain the higher m_e at the time (Online Resource 1a). *M. balthica* is known to be an active bioturbator (Volkenborn et al. 2012) and it may have contributed to an increased erosion rate through influencing sediment consolidation and hence facilitating erosion and resuspension of the muddy sediments.

At site I the τ_c values were highest in October, when also the abundance of *Hydrobiidae* dominated (Online Resource 1a). *Hydrobiidae* feeds on algae and detritus from the sediment surface and possibly prevented the formation of a ‘fluffy

layer' after the growth season and leaving the sediment relatively consolidated. This was also supported by the low m_c at the time. The stabilizing effect of the abundance of *Hydrobiidae* is in contrast to previous studies, which have shown that the *Hydrobiidae* destabilizes the sediment by grazing the stabilizing biofilm and producing “fluffy” faecal pellets (Austen et al. 1999; Andersen et al. 2002). It should be noted, however, that the stabilizing or destabilizing effects of an animal on sediment erodibility depends also on the context, i.e. organisms' influence on sediment erodibility may differ depending on, for example, the erosion stage or local habitat structure (e.g. sedimentary environment, vegetation density) (Joensuu et al. 2018). m_c also remained low in December at site I, suggesting that the grazing macrofauna may have decreased the quantity of easily eroding organic matter from the sediment surface. The observation of an effect of biota on sediment erodibility of muddy sediments was supported by our analysis and hence likely contribute to the clear temporal cyclicity in the resuspension potential metrics in this study.

At site II (mixed sediment), τ_c increased with the dry bulk density in contrast to sites I and III. Despite the low dry bulk density and high water content in April, τ_c was rather surprisingly two times higher in April compared to the lowest values of τ_c in June and December. Also, m_c was lowest in April indicating that the sediment was indeed very stable at the time. The positive correlation between τ_c and the microbial biomass variables suggests a microbial stabilizing effect. Similarly to site I, the organic content and microbial biomass variables were notably higher in April compared to other months (Online Resource 1b), but with a different influence on sediment erodibility. Since the sediment at site II is a mixture of mud and sand, the erosion dynamics differ from those of a more uniform grain sizes consisting of either mud or sand (Torfs et al. 2001; Sanford 2008). In general, the erosion rate of mixed sediment is higher compared to muddy or sandy sediment, because cohesive forces are negligible, but fine fraction are still relatively easily resuspended (Roberts et al. 1998).

Microbes (including diatoms) are able to produce EPS that can bind fine particles by adhesion forming flocs that increasing bed strength and resistance to erosion (Winterwerp and van Kesteren 2004). In addition, diatoms are able to migrate vertically, and it has been suggested they also stabilize the sediment in deeper layers (Holland et al. 1974). The flocs can also further aggregate to larger particles, which can reach the sizes up to 1000 μm (Stolzenbach et al. 1992). Hence, diatoms may have increased the sediment consolidation and resistance to erosion. As sediment consolidation is also generally higher in mixed sediment compared to muddy sediment, and it also increases with depth, the erosion rate may have decreased after the erosion of surface layer at site II. Furthermore, organic matter also enhances the cohesiveness of the sediment (Grabowski et al. 2011) and may form a structural, stabilizing layer on top of the sediment (Aberle et al.

2004). The variation in m_c was reflected in τ_c at site II indicating that the erosion process of the deeper layers of the sediment was mostly regulated by the variation in τ_c . Nevertheless, despite the occasional role of biota on sediment erodibility at site II, the dry bulk density was the best single predictor for sediment erodibility in the DistLM analysis.

In contrast, at site III (sandy sediment), there was little variation in the resuspension potential metrics, despite marked temporal variation in environmental conditions. Instead the higher variation in τ_c within the sampling time highlighted the heterogeneity of the sedimentary environment within the site. Site III was the most exposed and there likely experienced the greatest near-bed hydrodynamic forcing and the physical sediment properties were clearly the most important for the sediment erodibility at the site.

Sediment Resuspension and Its Impact on the Nutrient Concentrations in the Near Bottom Water

Coastal sediments are potential nutrient sources and since resuspension may release nutrients from the sediments, it is important to estimate its role in nutrient budgets but this has proven difficult because contradicting results have been reported (e.g. Tengberg et al. 2003; Almroth et al. 2009; Kalnejais et al. 2010; Wengrove et al. 2015). As resuspension entrains near-surface sediment pore water into the water column, in a heterogeneous coastal seascape its effects on the sediment-water nutrient exchange are likely to vary substantially in time and space. For example, coastal morphology, variation in hydrodynamics processes (waves, tides and currents), riverine or shoreline input of suspended solids and organic matter may all affect the nutrient dynamics at the sediment-water interface. Furthermore, differences in methodology (e.g. devices, experimental setup) may also partly explain the contradicting results. Our experiments mimic natural resuspension events where sediment erosion and transport are initiated by shear stress and turbulent water motions and thereby demonstrate the impact of the temporal and spatial variation in sediment resuspension on sediment-water exchange of nutrients in coastal sediments.

Although all sites were potential nutrient sources in our study, sediment resuspension only had a small impact on sediment-water exchange of nutrients in general. The nutrient concentrations in sediment pore water were highest at site I, but interestingly sediment resuspension had the clearest impact on nutrient fluxes at site II where, for example, the NH_4^+ concentration in the near bottom water increased by 93% on average (i.e. in April from 1.5 to 2.9 $\mu\text{mol L}^{-1}$) and $\text{Si}(\text{OH})_4$ concentration by 180% on average (i.e. in April from 2.1 to 5.9 $\mu\text{mol L}^{-1}$). Although the percentage change of NH_4^+ and $\text{Si}(\text{OH})_4$ concentrations in the near bottom water were sometimes high, in practice, the quantity of nutrients released from

sediments to the near bottom water was relatively low. At sites I and II, the positive change in the near bottom water nutrient concentrations of NH_4^+ and $\text{Si}(\text{OH})_4$ after resuspension experiments suggests, however, that there is a potential for sediment resuspension events to recirculate small amounts of these nutrients from the sediments to the overlying water. On the other hand, these sites are sheltered or moderately sheltered, and the likelihood of such events would require sufficient hydrodynamic forces to initiate sediment resuspension. During episodic storm events, the release of NH_4^+ and $\text{Si}(\text{OH})_4$ could, however, be important for fuelling local primary production, especially diatoms, which are limited by silica.

Sediment resuspension did not markedly change the PO_4^{3-} concentrations in the near bottom water at any of the sites. This may be partly explained by the fact that it is generally difficult to quantify the PO_4^{3-} release in oxic conditions, where it is easily adsorbed by iron oxides (Tengberg et al. 2003). Further, sediment resuspension did not have a significant impact on any of the nutrient fluxes at the sandy site III. In permeable sands nutrient concentration gradients from the sediment surface layer to the overlying water are small, because of the higher pore water exchange with the overlying water (Huettel et al. 2014), which may explain our results. The erosion depth in our experiments did not reach the deeper layers of the sediment and hence the quantity of pore water released was small and from the very surface layer of the sediment. In addition, pressure fluctuations caused by waves and near-bed hydrodynamics interaction with bottom topography may alter pore water pressure and hence further enhance the sediment-water column exchange of nutrients, especially at the sandiest site (III) (Santos et al. 2012; Huettel et al. 2014).

Our results suggest in the long-term, natural sediment resuspension events only have a minor role for nutrient release from sediments compared to diffusive transport, or the influence of fauna on these solute fluxes (e.g. Norkko et al. 2013). This is especially true in muddy and mixed sediments, where natural sediment resuspension events are less frequent and benthic macrofauna may substantially influence solute fluxes (Gammal et al. 2019). To put the significance of sediment resuspension for nutrient release into a context, we compared our resuspension induced fluxes of NH_4^+ and $\text{Si}(\text{OH})_4$ from site II to corresponding diffusive fluxes from the same study area and sediment type (Gammal et al. 2019). The concentrations NH_4^+ and $\text{Si}(\text{OH})_4$ in the overlying water after a resuspension event could be reached in approximately 20 and 70 min, respectively, via the diffusive flux of nutrients from the sediments. However, sediment resuspension may have an important role in oxygenating the surface sediment and influencing the biogeochemistry of the surface sediment and hence the subsequent biologically generated fluxes.

Our findings are similar to some of the previous findings from the Baltic Sea. Almroth et al. (2009) studied the effect of resuspension on nutrient fluxes in situ in the Gulf of Finland.

They found that sediment resuspension increased oxygen consumption but did not release significant amounts of nutrients from the sediments in oxic conditions similar to our observations from site III. Furthermore, Tengberg et al. (2003) reported rather similar results from the Göteborg archipelago, in the Baltic Sea. They also induced resuspension in situ and measured subsequent nutrient fluxes finding a significant increase in $\text{Si}(\text{OH})_4$ and decrease in PO_4^{3-} flux, while the NH_4^+ flux did not change markedly. Niemistö et al. (2018) conducted some in situ measurements of benthic fluxes (NH_4^+ , PO_4^{3-} , NO_x , $\text{Si}(\text{OH})_4$ and O_2) in the same area in the Gulf of Finland, close to our study location. They had two stations (7 m and 20 m depth) where measurements were made once in May and August. They found that sediment resuspension increased oxygen consumption and impacted on nutrient fluxes mainly in August by increasing the influx of NH_4^+ and $\text{Si}(\text{OH})_4$ at the 7 m station and PO_4^{3-} at the 20 m station, and efflux of NO_x at both stations. However, the number of replicates was very low (1 or 2 per time/site) and they also conducted markedly stronger resuspension experiments in August, which may have affected their results.

Conclusions

In this study, we covered most of a seasonal cycle, and although our results are snapshots in time, they do demonstrate how the dynamic changes in environmental conditions are reflected in sediment characteristics and erodibility. Our findings show the importance of temporality on sediment erodibility, particularly in muddy sediments. While bulk density may turn out to be a relatively accurate predictor for sediment erosion in sandy sediments, our results highlight that temporal variation in biota is particularly distinct in muddy sediments and should be accounted for. However, physical and biological sediment characteristics are inevitably interlinked and therefore it is difficult to determine from this study exclusive single predictors (or drivers) of sediment erodibility. More specific studies focusing on the co-correlations among key environmental variables would provide insights on their direct and indirect effects on sediment erodibility. It would also be important to investigate the impact of land-sea interactions (e.g. direct and indirect effect of riverine discharge) and include hydrodynamic measurements to quantify resuspension regimes. Even though our findings are restricted to the shallow areas, these are also the areas which are particularly prone to natural resuspension events. Nevertheless, the contrasts in resuspension potential between our sites were quite large, which suggests that it could be important to include more subtidal environments into temporal studies (differences in depth, salinity, vegetation and benthic communities) in the future.

In addition, more long-term research is required on the temporal trends of sediment erodibility and resuspension in order to predict and manage sediment transport in coastal areas and its impact on morphology and ecological processes affecting society.

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