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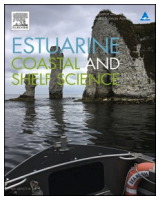
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Coarsening coasts: quantifying sensitivity of benthic communities to sandification

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ABSTRACT

Sea level rise, increased storminess, and changes in sediment supply due to nourishments are all expected to drive coarsening (i.e., 'sandification') of muddy coastal sediments in the decades to come. Since the composition of soft-bottom benthic communities is associated with the sediment grain-size and mud content, this may result in habitats becoming less suitable for some species, leading to species shifts. **Species-sediment relations** can help to predict how this foreseen sandification may affect benthic fauna. We explore and quantify the sandification-sensitivity of benthic communities, with a tidal basin in the Dutch Wadden Sea as a model system. We identify the species' sediment optima and tolerance ranges using **non-linear quantile regression models**, summarise preference and sensitivity at the community level, and determine the difference between optimal and realised sediment habitat. We find that sediment optima are taxon-specific and that most species in this area are sediment generalists. On community level, there is a difference between the preferred and realised sediment habitat. In many areas, the actual inhabited sediment is **coarser and sandier** than expected based on the preferences of the resident species. Future sandification of the area would further decrease sediment habitat suitability for benthic communities in these places. This detailed knowledge of area-specific sensitivity of benthos can be used to inform coastal management decisions.

1. Introduction

Soft-sediment coastlines may be expected to coarsen in the decades to come – a process which can also be referred to as 'sandification'. Firstly shallow coastal areas are increasingly affected by sea level rise and storminess, both resulting in larger waves hitting the coasts and hence coarsening of sediments (Ranasinghe, 2016; Ranasinghe et al., 2013). Secondly, humans have altered sediment fluxes on a global scale (Syvitski et al., 2022). By modifying sediment supply, anthropogenic activities can regionally result in coarser sediment. For example, fine sediment input to the sea is strongly reduced by river damming (Syvitski et al., 1979; Dethier et al., 1979) and sand mining (Jordan et al., 2019). Between 1950 and 2010, the land to sea flux of sediment has been reduced by 23 % (Syvitski et al., 2022). On the other hand, the supply of coarse sediment has increased by sand nourishments (de Schipper et al., 2021; Huisman et al., 2018). To compensate for rising sea levels and coastal erosion, the need for sand nourishments has strongly increased over the last decades and will keep growing (Brand et al., 2022; Vousdoukas et al., 2020). These structural additions of large volumes of sand may alter the sediment supply to and composition of connected coastal systems (de Schipper et al., 2021). Sandification could have major implications for the ecological functioning of such systems. We use a protected UNESCO World Heritage – The Wadden Sea – as example to assess the role of sandification on ecology.

The Wadden Sea is a shallow coastal sea in Western Europe, bordered by barrier islands. Its habitats range from muddy intertidal flats and

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sand banks to deep gullies characterized by coarser sediment and high current velocities. Especially the muddy intertidal flats and sand banks give this area a unique ecological value (Reise et al., 2010). Primary productivity by benthic micro-algae (Christianen et al., 2017), combined with advection of organic matter from freshwater sources (Jung et al., 2019), support a high macrozoobenthic biomass (Beukema and Dekker, 2020) on which large (migratory) bird populations feed (Zwarts and Wanink, 1993). In the Wadden Sea, both the sand budget of the coast and the transport capacity through its tidal inlets determine sediment transport into the basin and towards the tidal flats (Wang et al., 2018). The North Sea coastline of several of the Wadden islands is structurally nourished with large volumes of sand, and also new types of nourishments are being developed and applied (Lodder et al., 2023; Perk et al., 2019). However, long-term and far-field ecological effects of such nourishment programmes on sediment composition and their influence relative to that of natural sediment transport processes are not well-understood yet (Staudt et al., 2021; Speybroeck et al., 2006). Although no general sandification trends were observed in the Dutch part of the Wadden Sea over the period 2009–2019 (Folmer et al., 2023), the eastern part of the Wadden Sea may already be mud-limited, i.e. the supply of suspended mud is lower than the accommodation space for deposition, and this mud deficit is expected to increase under sea level rise (Colina et al., 2024; Dolch and Hass, 2008). Therefore, the Wadden area is at high risk of sandification.

Soft-bottom benthic species are linked to the sediment they inhabit (Gray, 1974; Young and Rhoads, 1971) and the composition of benthic communities can largely be explained by sediment median grain size and mud content (Van Colen, 2018; Compton et al., 2013; Ysebaert and Herman, 2002; de Jong et al., 2015). Also functional traits, such as feeding mode and burrowing capability, show relationships with preferred sediment (Gusmao et al., 2022). Each species has its own preferred optimum for grain size and mud content (Anderson, 2008; Armonies, 2021; Cozzoli et al., 2013; Kraan et al., 2010). Some are, however, more specialised than others (Robertson et al., 2015). In other words: their niche breadth differs. Following ecological theory, a species' niche optimum is defined by the conditions under which the highest abundance or biomass can be achieved, while niche breadth is defined by the range of conditions that a species can tolerate (Hutchinson, 1957; Treurnicht et al., 2020). Whereas generalists have a broad niche and can reach high biomass along a range of environments, habitat specialists are most affected by changing environmental factors (Rodil et al., 2018; Pandit et al., 2009). The proportions of generalist and specialist species in a community can determine the ecosystem functioning and recovery after disturbance (Richmond et al., 2005). Therefore, the niche breadths of individual species can be used to define ecosystem sensitivity and hence robustness to environmental change.

Defining accurate species-sediment relations remains challenging. Firstly, multiple variables affect both sediment composition and benthos distributions. Sediment grain size composition and organic matter content is correlated with, amongst others, hydrodynamics: fine-grained sediments are found in low-stress hydrodynamics conditions and contain higher amounts of organic matter, while coarser sediments are poor in organic matter and are present under higher hydrodynamic stress. This co-variation complicates description of the causation between sediment and community composition (Snelgrove and Butman, 1994). Species distributions are, in turn, associated with multiple environmental variables like hydrodynamic stress (Herman et al., 2001) exposure time of intertidal flats (Kraan et al., 2010) and food availability (Herman et al., 1999), as well as with other biotic interactions such as predation and competition (Bijleveld et al., 2015). The benthic fauna themselves can also influence sediment composition, for instance by their burrowing activity or physical structure (Meadows et al., 2012; Rhoads and Boyer, 1982). In practice, acquiring measurements or reliable estimates of all these ecologically relevant variables is challenging.

Several statistical modelling approaches deal with the problem of many confounding, unmeasured variables in ecological research. One of them is quantile regression (Koenker and Bassett, 1978; Cade and Noon, 2003). With quantile regression, all quantiles of a species' distribution over a parameter of interest are determined, without assuming a parametric distribution of the model error. The upper quantiles of a species' distribution over the parameter of interest reflect the instances where all other, unmeasured, parameters are least constraining, representing the "ecological factor ceiling" (Thomson et al., 1996), which is an indication of the potential species distribution (Vaz et al., 2008). Quantile regression has been proposed as a suitable technique for modelling benthos-sediment relationships in several studies (Anderson, 2008; Cozzoli et al., 2013; Chauvel et al., 2024). These studies investigated community composition over a mud gradient, the relative importance of coarse sediments for benthic communities, and differences in species sediment preferences between basins. However, to date, these approaches have not yet been employed to quantify species and community sensitivity to sediment composition. It largely remains to be investigated exactly how sensitive benthic communities are to a change in sediment composition, and how their current distribution relates to their potential sediment habitat.

In this study, we quantify sediment preferences of macrozoobenthos and their potential sensitivity to changes in sediment composition, to explore how benthic communities may respond to sandification resulting from climate change effects and coastal engineering. Our goal is to estimate *where* changes in sediment composition may have the strongest implications for community composition and *which species* will be most affected. Based on the location of the optimum, and on the width of non-linear quantile regression curves, we classify species as sand or mud-preferring and sediment generalists or specialists. We then combine the optima of the different species, weighted according to their relative abundance in a community, to derive the preferred community optimum. Comparison of the preferred and actual sediment habitat then indicates suitability of the sediment composition for that community and can be used to identify sensitivity hotspots, where further changes may affect benthic communities most. Pinpointing these sensitivity hotspots for sediment change may inform coastal management decisions on nourishment locations and substrate. We apply this method to a case study of the Ameland inlet and tidal basin in the Dutch Wadden Sea.

2. Methodology

2.1. Case site description: the borndiep tidal basin, Dutch Wadden Sea

The Borndiep (53°N 5°E) is a tidal basin in the Dutch Wadden Sea, connected to Ameland tidal inlet and bordered by the tidal divides under the islands of Terschelling and Ameland. The basin is approximately 25 km wide between the two tidal divides, and approximately 15 km long from the inlet to the mainland coast. Anthropogenic activities within the area include fishing, sand nourishments and dredging. Shrimp trawlers visit the deeper subtidal parts 3–9 times per year (Rippen et al., 2021). The navigation channel between Ameland and the mainland requires daily dredging to remain accessible for ferries, amounting to a yearly dredged volume of nearly 2 million m^3 (Rijkswaterstaat, 2022). In 2018, a 5 million m^3 nourishment was placed at the outer edge of Ameland ebb-tidal delta, located on the North Sea side of Ameland inlet, to stimulate natural sand supply to the northwestern tip and North Sea coast of the island, which suffers from ongoing erosion. This mega-nourishment affected the local benthic communities at the nourishment site, but monitoring of the fauna showed that these communities largely recovered after 3 years (Escaravage, 2022). However, it remained unclear if and to what extent the nourishment influenced the fauna deeper into the tidal basin.

2.2. Benthos and sediment sampling

To test sediment preference and sensitivity of benthic communities, we use faunistic data collected between 2015 and 2020. These samples

were taken from intertidal flats, subtidal gullies, and the ebb-tidal delta, the area just outside the inlet (Fig. 1). The sampled area covers a wide range of sediment types and environmental conditions.

Benthos and sediment samples were collected as part of the intertidal and subtidal benthic surveys performed by the Royal Netherlands Institute of Sea Research (NIOZ). Intertidal data was obtained through the synoptic intertidal benthic survey (SIBES; (Bijleveld et al., 2024; Bijleveld et al., 2025)). This dataset covers 639 sampling stations in the Ameland Inlet, of which 525 are located on a regular 500 × 500 m grid and 114 are randomly placed (Bijleveld et al., 2012). Stations were sampled by foot with a hand core (0.0177 m^2 surface area) or by RIB combining two long cores (0.0175 m^2 combined surface area). For details on the sampling procedure, we refer to Compton et al. (2013) and Bijleveld et al. (2025). Subtidal samples were collected as part of NIOZ subtidal sampling campaigns and within the projects TRAILS and WaddenMosaic (Franken et al.). Subtidal stations, 145 on a 1000 × 1000 m grid and 41 randomly placed, were sampled by ship with a boxcore (0.06 m^2 surface area) or by zodiac boat combining 4 long cores (0.035 m^2 combined surface area). For more details on the subtidal sampling, we refer to Franken et al. (Franken et al.). In Fig. 1, an overview of all 2991 samples, mapped per year and season, is given.

Sediment samples were taken from the top 4 cm of the sediment and stored at −20 °C. Prior to analysis, the samples were freeze-dried, homogenised with mortar and pestle, weighed and added to auto-sampler tubes with degassed reverse osmosis water. Grain size composition was determined with a laser diffraction particle size analyser (Coulter LS 13320).

Benthos samples were sieved using a 1 mm mesh size and all material and fauna remaining on the sieve were stored at 4–6 % formaldehyde, buffered with borax and stained with Rose Bengal (CAS Number: 4159-77-7). In the laboratory, all macrozoobenthos were sorted out of the sample and identified to the lowest possible taxonomic level. Per taxon, dry weight was determined after oven drying them for 2–3 days at 60 °C and ash free dry weight was measured after 5 h combustion at 560 °C. For details on the laboratory procedure, we refer to Compton et al. (2013) and Bijleveld et al. (2025). For our main analysis, we focused on the abundance data, as biomass could not be established for all species because samples sometimes contained only a limited number of individuals with a small body size, which therefore fell below the detection limit of the scale. We validated our findings by repeating the analysis with the available biomass data.

2.3. Sediment composition and other environmental variables

To explore whether sediments changed over the studied period, we tested for trends of both median grain size (d_{50}) and mud content. We constructed linear regression models of sediment composition over time (year) for all stations which were sampled at least 3 times and mapped the slope parameters of all significant regressions.

We explored the correlations between d_{50}, mud content and several other environmental variables. Elevation data were obtained from the bathymetric survey done by Rijkswaterstaat in 2015. Mean salinity, salinity variation, current velocity and bed shear stress were obtained from the Dutch Wadden Sea Model (DWSM) in Delft3D-Flexible Mesh (FM) (Van Weerdenburg, 2024). Bed level change since 2014 was obtained from a stratigraphic model (Pearson et al., 2020). To explore the significance of d_{50} and mud % as predictors of community composition, we performed a redundancy analysis (RDA). Benthos abundance data was transformed to relative abundance, i.e. the number of individuals per species was divided by the total number of individuals in the sample. Environmental data was standardised by centring and scaling. We checked environmental variables for collinearity using variance inflation factors (VIFs). A higher VIF value means a stronger collinearity with other variables. We sequentially eliminated variables with the highest VIF, until all variables showed VIF below 10 (Montgomery and Peck, 1992). This resulted in the removal of current velocity and mean salinity. We performed stepwise forward and backward selection of variables, with 999 permutations for each test and a *p*-value threshold for inclusion at 0.05 and for exclusion at 0.1. Next, we tested the significance of the resulting RDA and each selected variable (d_{50}, mud %, salinity variability, bottom shear stress, orbital velocity, elevation and bed level change) through permutation tests, with 999 permutations.

2.4. Species-sediment relations by quantile regression

Quantile regression enables to study differential responses of benthos over sediment of different ends of a species' distribution. When multiple variables are limiting abundance, the top quantiles reflect the instances

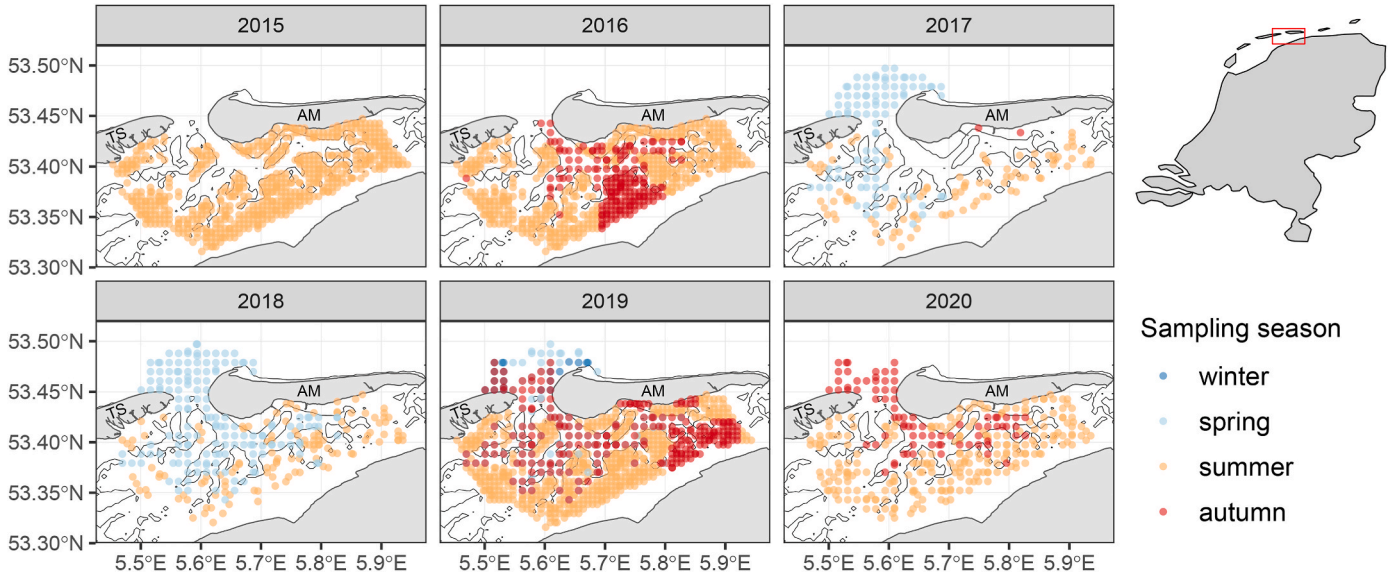


Fig. 1. Overview of all samples used in this study. The inset shows the Netherlands, with the sampling area indicated by the red box. The Borndiep tidal basin and Ameland inlet are located between the islands of Ameland (AM) and Terschelling (TS). The ebb-tidal delta, sampled from 2017 onwards, lies on the north side of the inlet. The gully outlines are shown by the black contour line. Data point colour indicates in which (meteorological) season the samples were taken. Note that in 2019, the subtidal areas were sampled twice: in spring and autumn.

in which all variables are supposedly least limiting. Therefore, these quantiles are the best representation of the potential species distribution over the variable of interest (Cade and Noon, 2003). We use the $\tau = 0.95$ quantile, representing the value under which 95 % of the observations is expected to fall. This 95th quantile strikes a balance between displaying the upper end of the taxon's distribution, and minimising the effect of outliers, to which higher quantiles are sensitive (Anderson, 2008; Cade et al., 1999).

Here we are interested in the role of grain size and mud percentage. The dataset needs to be sufficiently large to encompass optimal conditions for all measured and unmeasured variables over the gradient of interest. As the extensive sampling schemes cover the whole tidal basin, this guaranteed that we captured all possible abiotic gradients. Samples were taken from inter- to subtidal locations, and from muddy to sandy sediments characterized by high to low-dynamic conditions. However, as the sampling resolution between the intertidal and subtidal areas in the original data sets differed, 78 % of the samples were from the intertidal. To correct for spatial autocorrelation and to balance the number of inter- and subtidal stations, the data was spatially resampled with a minimum distance between stations set to 750 m. This resampling, which was repeated 100 times, resulted in subsample datasets with on average 1150 samples, of which approximately 60 % were intertidal stations. See Fig. S1 for an example of a spatial subset.

Fitting the upper quantiles can be problematic when data density is low. Therefore, only taxa occurring in at least 10 % of the samples were selected for quantile regression model fitting, which resulted in the selection of 22 taxa. Furthermore, to prevent overestimation of abundance at the extremes of the sediment gradient, where data was also scarce, we removed the lower and upper percentile of d_{50} observations and the upper percentile of mud content observations. Absences of biota observations were assumed to reflect unsuitable habitat conditions. Therefore, zeros were included in the analysis, although these have a minimal influence on the modelled relationship when using the 95th quantile (Cade et al., 1999).

Since benthos-sediment relationships are generally not linear, we constructed non-linear quantile regression models using B-splines (Koenker et al., 1994; Thompson et al., 2010). With B-spline smoothing, piecewise polynomials of a specified degree are fitted without predetermining curve shape by a function. For selecting the appropriate polynomial spline degrees, we used Akaike's information criterion corrected for small samples (AICc) (Burnham and Anderson, 2004; Hurvich and Tsai, 1990). As suggested in previous studies (Anderson, 2008; Cozzoli et al., 2013; Cade et al., 2005), we fitted models with 2, 3, 4 or 5 spline degrees and selected the model with the lowest AICc. To further smoothen the model fit, we used a lasso algorithm (Tibshirani, 1996), with parameter lambda = 1. The R code for constructing the quantile regression models can be found in the appendix (Supplement B).

The spatial resampling followed by quantile regression model fitting was performed 100 times. For individual taxa, the maximum abundance of the 95th quantile distribution demarcated the sediment optimum. We defined the minimum and maximum of the optimum tolerance range by the sediment composition at a curve cutoff of 25 % of the abundance optimum (Fig. 2). The optimum and minimum and maximum tolerance per taxon were calculated, averaged over all rounds of resampling.

2.5. Community sediment sensitivity

For each sample, we estimated the community weighted mean sediment optimum (CWM_{d50} and CWM_{mud}). This was done as follows (eq. (1)), weighing the sediment optima (*opt*) by the relative abundances (*w*) of each taxon *i* in that specific sample:

$$CWM = \sum_{i=1}^{n} (opt_i \cdot w_i) \quad (1)$$

We then determined the difference between this inferred community sediment optimum and the actual sediment composition for each sample, with respect to the d_{50} and mud content (Δ_{d50} and Δ_{mud}; eq. (2)):

$$\Delta_{d50} = d_{50} - CWM_{d50} \quad \text{and} \quad \Delta_{mud} = mud\,\% - CWM_{mud} \quad (2)$$

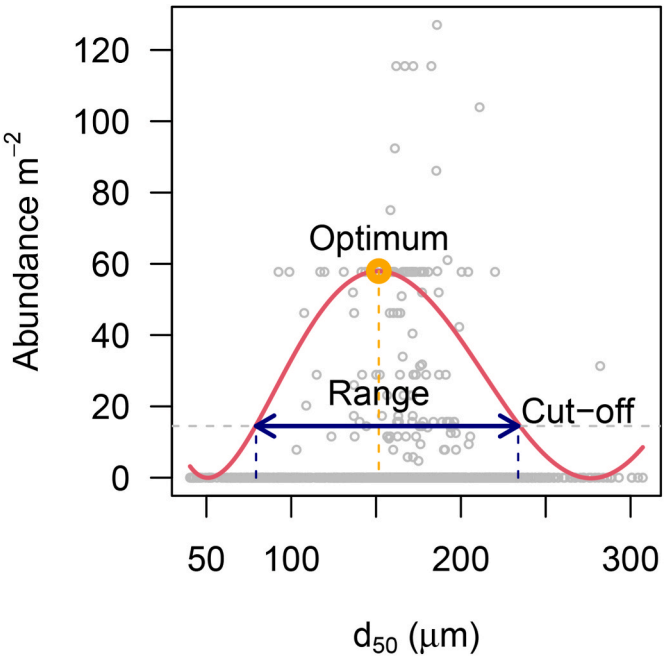


Fig. 2. Conceptual illustration of the derivation of the taxon sediment preference. Indicated are sediment optimum (yellow circle) of the 95th spline regression quantile (red curve), and range (blue arrows), determined by the curve width at a cutoff of 25% of the optimal abundance. The observations, including zero's, are plotted in grey.

We compared the distributions of these residuals for the intertidal and subtidal area and mapped the mean value per station over the entire study period. For each sample, we also determined which fraction of the taxa occurred outside their preferred sediment range.

All analyses were performed in R version 4.4.1 (R Core Team, 2024), with the packages "vegan" (Oksanen et al., 2024) for multivariate analysis, "quantreg" (Koenker, 2024) for fitting quantile regression models, and "spatialEco" (Evans and Murphy, 2023) for spatial subsampling.

3. Results

3.1. Sediment and environmental variables

Sediment was finest on the intertidal flats near the mainland coast (Fig. 3a and d). The coarsest sediments are found in the deeper subtidal gullies in the basin and at the ebb-tidal delta outside of the inlet. Median grain size (d_{50}) ranged from 19 to 431 µm with a median of 161 µm, and mud fraction ranged from 0 to 81 % with a median of 6 %. Sediment composition did not show distinct linear temporal trends over the studied period for the entire basin (Fig. 3b and e), nor did we observe spatial patterns in coarsening or fining during our study period (Fig. 3c and f).

Mud content and d_{50} were related, and showed correlations with elevation, salinity and hydrodynamics (see Fig. S2 for correlations between all parameters). The RDA analysis ($R^2_{adj} = 0.14$, $p = 0.001$; Table S1) showed that mud content was the main variable driving community composition. The first RDA axis (explaining 7.8 % of the total variation) was mostly related to sediment composition, while the second axis (explaining 4.6 % of the total variation) was mostly related to elevation and bottom shear stress (Fig. S3).

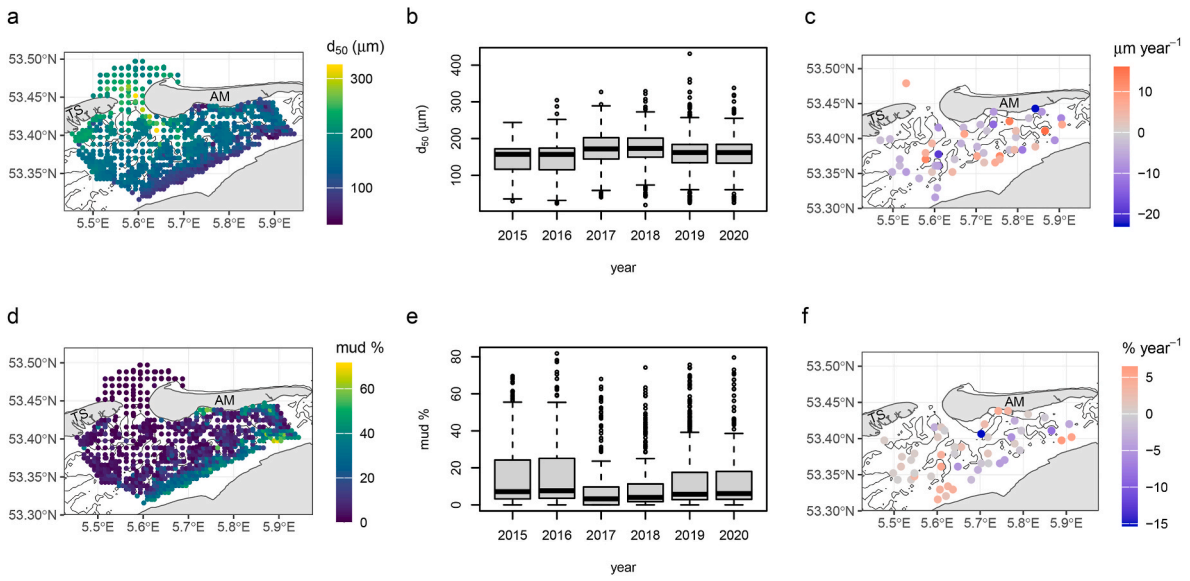


Fig. 3. Spatial and temporal distribution of sediment composition: (a) mean d_{50} and (d) mud content per station over all sampled timepoints; boxplot of (b) d_{50} and (e) mud content per year; and trends in (c) d_{50} and (f) mud content, quantified as the slope of (significant) linear regressions of sediment composition over time.

3.2. Species sediment relations

For the 22 most abundant taxa, clear abundance maxima of the 95th quantile for both d_{50} and mud content were found (see for example quantile regressions Fig. S4, and for a table containing all optima and sediment ranges Table S2). Fig. 4a (d_{50}) and c (mud) show that taxon sediment optima range from coarse to fine sediment. For instance, *Nephtys cirrosa*, *Magelona mirabilis* and *Scoloplos armiger* show sand preference while *Hediste diversicolor*, *Heteromastus filiformis* and *Macoma balthica* show mud preference.

There are large differences in the tolerance ranges of different species. Generalist species with the largest tolerance ranges (wider than 200 µm) are *Hediste diversicolor*, *Arenicola marina* and *Nereididae*. More specialised species like *Urothoe poseidonis*, *Lanice conchilega* and *Nephtys hombergii* have a tolerance ranges smaller than 100 µm (Fig. 4a).

Species with a preference for sand (e.g. *Magelona johnstoni*, *Magelona mirabilis* and *Nephtys cirrosa*) have generally narrower tolerance ranges than species with a preference for mud (e.g. *Hediste diversicolor*, *Heteromastus filiformis* and *Macoma balthica*). This is reflected in a negative relationship between sediment grain size optimum and tolerance range (Fig. 4b), and a positive relationship between optimal mud content and tolerance (Fig. 4d).

Sediment optima calculated based on biomass data show a strong relation with abundance-based optima (Fig. S5). Only for a few taxa, biomass and abundance optima differ. Several species have a higher d_{50} optimum (most pronounced in *Arenicola marina*, *Hediste diversicolor*, *Nephtys cirrosa*, *Magelona mirabilis* and *Magelona johnstoni*) or a lower mud content optimum (*Hediste diversicolor*, *Heteromastus filiformis* and *Macoma balthica*) for biomass compared to abundance. This means that these species reached their highest biomass in coarser sediment, compared to where they reach their highest abundance. *Marenzelleria viridis* is the only species with a pronounced sandier abundance optimum and muddier biomass optimum.

3.3. Community sediment preference and sensitivity

The mean community weighted optimum for median grain size (CWM_{d50}) ranges from approximately 50 to 270 µm (Fig. 5b). In the intertidal zone, CWM_{d50} lies most frequently below 150 µm while in the subtidal Wadden Sea and in the ebb-tidal delta, optima above 150 µm occur more frequently. CWM_{mud} displays peaks at 0 % mud, mostly representing subtidal stations containing benthos with a sand preference, and between 10 and 20 % mud.

The difference between the CWM_{d50} and the actual d_{50} (Δ_{d50}) per sample is skewed to the right, i.e., in many places the sediment is coarser than the optimum of the actual community. This difference is most pronounced in the intertidal zone. In the subtidal, Δ_{d50} is centred around 0 (Fig. 5c). The average Δ_{mud} has a negative skew (Fig. 5f). This suggests that actual mud content lies below the preferred optimum of the communities. Again, this skewness is most pronounced in the intertidal but also present in the subtidal.

Looking closer at which taxa are responsible for these community-level patterns, we found that the distribution of more than half of the surveyed taxa is skewed towards coarser than optimal sediments (Fig. S6). For a few, mainly sand-preferring, taxa (*Bathyporeia pelagica, Scoloplos armiger, Nepthys cirrosa*, *Magelona mirabilis* and *Magelona johnstoni*), sediment was often finer than optimal. Taxa for which the sediment preference matched the actual sediment characteristics, i.e., the distribution of Δ_{d50} and Δ_{mud} was centred around 0, are *Capitella* sp. and *Ensis leei* for d_{50}, and *Spio martinensis* and the sand-preferring taxa for mud content.

Temporally, neither Δ_{d50} nor Δ_{mud} showed linear trends over the studied period (Fig. S7).

3.4. Spatial patterns

There are coherent spatial patterns in the distribution of both Δ_{d50} and Δ_{mud} (Fig. 6a and b). Stations in the intertidal and subtidal zone as well as stations in the ebb-tidal delta have positive values for Δ_{d50}. This indicates that the actual d_{50} is above the community optimum that is calculated based on the preferences of individual species. Also, stations from the watershed south of Terschelling show a mismatch towards coarser grainsizes. In contrast, along the mainland coast, at the watershed south of Ameland and in several stations near the southern coast of Ameland, d_{50} is below the community optimum (negative Δ_{d50} values), denoting finer than optimal sediments. In line with this, Δ_{mud} is negative for most stations, i.e., mud content is below the level which would be expected based on the average community preference (Fig. 6b).

Locations where the actual sediment composition lies beyond the optimal range for a large fraction of the present community are spatially clustered. At the intertidal areas south of the eastern part of Terschelling as well as the western part of Ameland, the d_{50} is larger than the

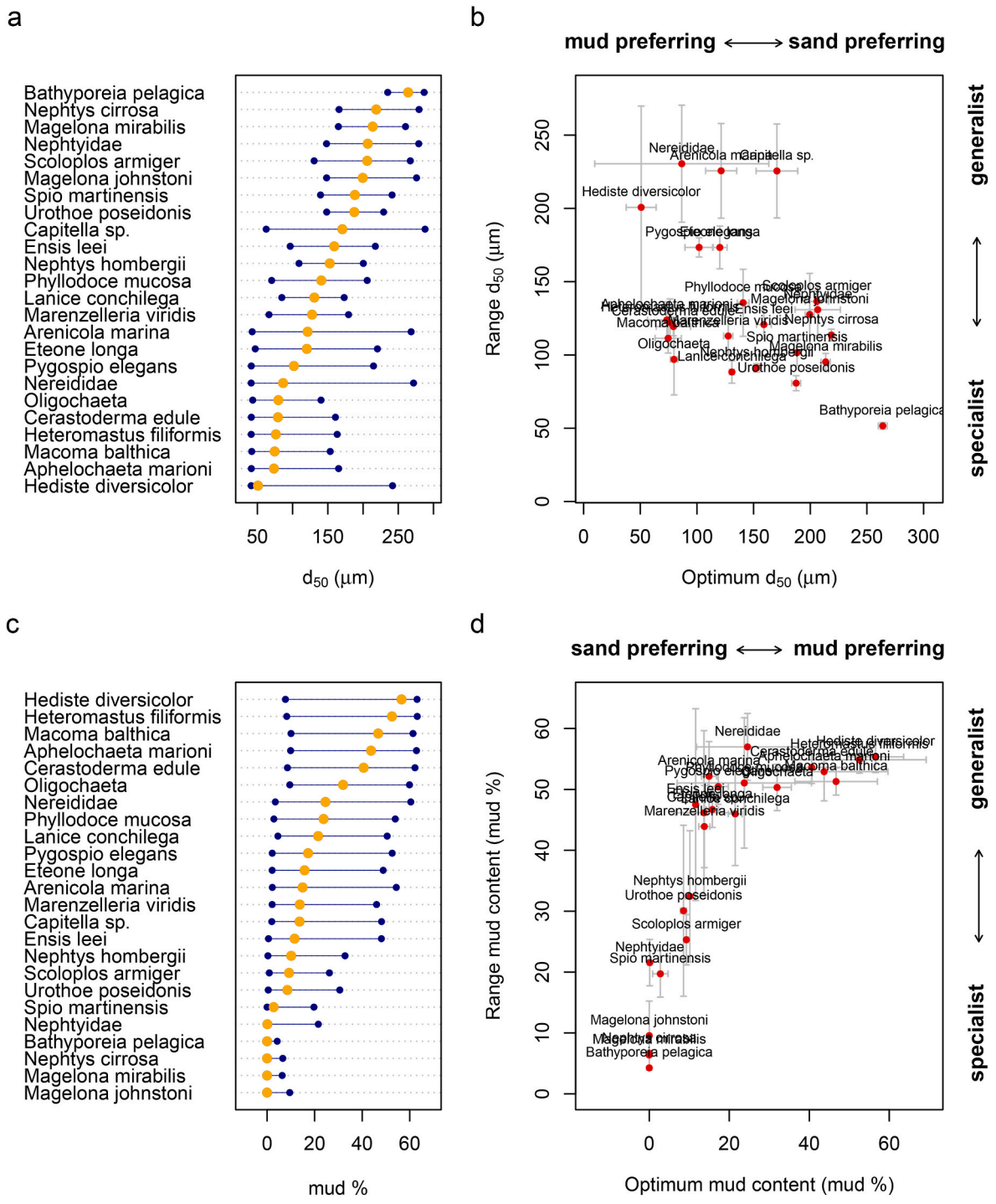


Fig. 4. Taxon-specific sediment preferences. (a) d_{50} and (c) mud content optima (orange dot) and range (blue segments) for taxa selected for this study. Position of optimum (b) d_{50} and (d) mud content compared to tolerance range, which indicates the level of sediment preference and specialisation. Error bars in b and d show the standard deviations of optimum and range over 100 spatial subsampling permutations and consecutive quantile regression model fitting.

optimum range of significant fractions (up to approximately 75 %) of the present species (Fig. 6d). The stations where d_{50} is finer than preferred are located at the ebb-tidal delta and the ends of the gullies south of Ameland (Fig. 6b). Mud content is lower than the sediment preference range of >25 % of the community at large parts of the intertidal area, except in the regions close to the mainland coast and the watershed south of Ameland (Fig. 6e). Only at a few stations, mud content is above the preference range for fauna (Fig. 6f).

4. Discussion

In what follows, we will first address methodological considerations, before placing our findings in an ecological context and discussing implications.

4.1. Validity of benthos-sediment relations using quantile regression

Quantile regression is still not widely applied in benthic ecology, one of the reasons being that sufficiently large datasets containing samples

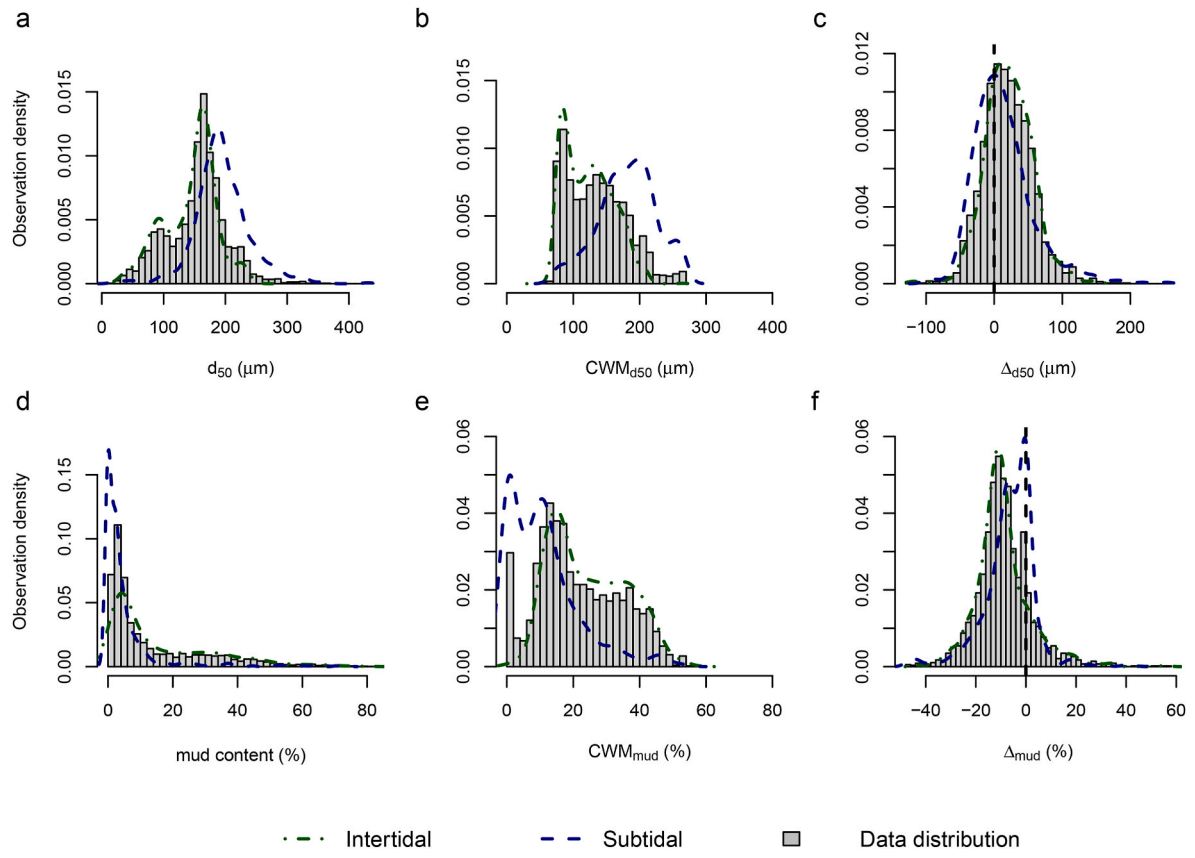


Fig. 5. Distribution of sediment composition, community optimum and community-sediment mismatch. The observation density for (a) d_{50} and (d) mud content; (b) community weighted mean (CWM) optimum d_{50} and (e) mud content; and (c and f) difference between sediment composition and CWM optimum per station (Δ_{d50} and Δ_{mud}, respectively).

over the environmental gradient are required to capture the complete biological response. In the current study, we had access to such a dataset. By using non-linear regression splines of the 95th quantile, we derive benthos-sediment relations which are robust to outliers and covariates and flexible in shape. Compared to previous quantile regression applications in benthic species distribution modelling (Anderson, 2008; Cozzoli et al., 2013, 2014, 2017; Vaz et al., 2008; Chauvel et al., 2024), our approach has several additional advantages. Firstly, spatial resampling allowed us to obtain error margins of the predicted model parameters, besides correcting for spatial autocorrelation and balancing the amount of inter- and subtidal data. Furthermore, summarising taxon-derived optima and tolerance on community level enabled us to scale up sensitivity predictions to the entire macrozoobenthic community. Nevertheless, a few limitations of the method should be considered.

Firstly, we assumed that the range of observations in our study contained the optima for all abiotic variables present within our dataset. However, within a single system, this is rarely the case (Thrush et al., 2005). For constructing more reliable benthos-sediment relations, data from different systems with a wider range of environmental conditions is desirable. Secondly, by using the highest quantiles as a reference of maximum species abundance over the sediment gradient, we assume other variables to be constraining. The highest quantiles describe the relation with the sediment less accurately when many facilitating rather than limiting processes are at play (Cade et al., 2005). This may be the case in the intertidal Wadden Sea, where facilitating biotic interactions, such as provided by habitat builders are prevalent (Rademaker, 2024). Furthermore, although here we related biota to gradients in sediment composition, some relevant sediment properties, such as cohesiveness, change abruptly rather than gradually (Van Ledden et al., 2004; Colina et al., 2022). This quality is not linearly reflected in the d_{50} or mud content, therefore we recommend for future studies to look further than these commonly used proxies. Lastly, the methods used in this study describe patterns rather than causation. Not all animals are solely subject to the physical dynamics of the sediment they live in. Some do also actively modify sediment composition, so that benthos-sediment relations are often two-way interactions. For instance, *A. marina* has been described to coarsen the sediment (Volkenborn et al., 2009; Wendelboe et al., 2013), and *C. edule* to increase fine sediment resuspension (Li et al., 2017) with their destabilising burrowing activity. Through bioturbation, benthic fauna can modify the morphology and sediment composition of their sedimentary habitat on a large scale (Brückner et al., 2025; Cozzoli et al., 2021). However, it remains to be investigated, whether by this bioengineering organisms actually create their preferred sediment habitat (Soissons et al., 2019).

The taxon optima and ranges we defined with the 95th quantile, reflect the potential rather than the realised sediment habitat (Vaz et al., 2008). The actual species' distribution is determined by a myriad of other limiting variables. To gain a mechanistic understanding of why species occur in suboptimal sediments, experimental studies testing interactions with other variables such as food availability, hydrodynamics and interspecific interactions are needed. In suboptimal sediment conditions, species and communities are less resilient to other stressors, such as climate-change related heat waves and storms (e.g. St-Onge et al. (2007)). To understand the eco-physiological implications for benthic species living outside of their preferred sediment habitat, multiple-stressor experiments are needed.

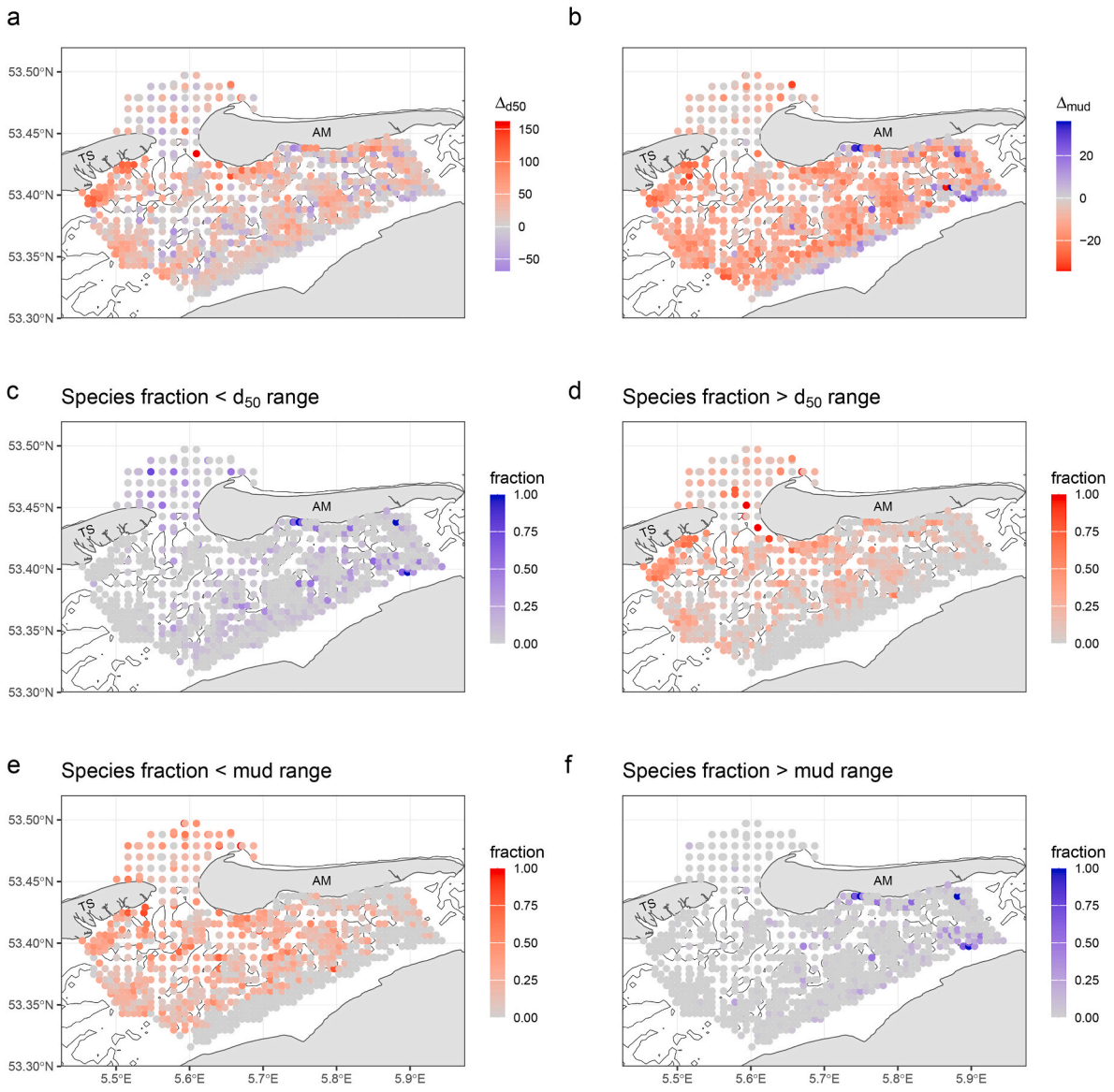


Fig. 6. Spatial patterns in sediment sensitivity. The differences (a; b) between sediment composition and CWM optimum per station, Δ_{d50} (μm) and Δ_{mud} (%), indicate whether the sediment is coarser/sandier (red) or finer/muddier (blue) than optimal for the present community. The fraction of the present taxa occurring (c) below or (d) above their d_{50} range, i.e. for which the sediment is almost too fine (blue, c) or too coarse (red, d). The fraction of the present taxa occurred (e) below or (f) above their mud content range, for which the sediment is nearly too sandy (red, e) or too muddy (blue, f). All values shown are averaged over all sampled time points per station.

4.2. *Most species show sediment preference but few show exclusivity*

The order of taxon sediment preference from fine to coarse corresponds to previously described sediment associations of benthic fauna in a comparable geographical area (amongst others, Armonies, 2021; Cozzoli et al., 2013; Nehmer and Kröncke, 2003; Reiss and Kröncke, 2001). Although in most cases, calculated sediment preferences based on biomass corresponded well to preferences based on abundance, we observed differences for a few taxa. These discrepancies might be related to ontogenetic changes in habitat preferences. For instance, for *A. marina*, the differential sediment optima for biomass compared to abundance suggests that fewer but larger individuals are found in coarser sediments. This can be linked to secondary migration of this species from high in the intertidal, where they live as juveniles, to lower in the intertidal for the adult life stage (Beukema and De Vlas, 1979). Besides ontogenetic changes in habitat preference, sediment composition may relate to differential growth rates or maximum body size (Witbaard et al., 2001).

While most species considered in this study had wide tolerance ranges, only a few taxa could be considered true sediment generalists. Only 4 taxa (Nereididae, *A. marina*, *Capitella* sp. and *H. diversicolor*) had a d_{50} range wider than 200 μm; and only 3 taxa (Nereididae, *H. diversicolor* and *H. filiformis*) had a mud range wider than 55 %. Likewise, Armonies (2021) observed few sediment generalists among North Sea benthos. We did not identify true sediment specialists either: d_{50} tolerance ranges were wider than 80 μm for all taxa but one (*B. pelagica*); mud content tolerance ranges were wider than 20 % for all but four taxa (*N. cirrosa*, *M. johnstoni*, *M. mirabilis* and *B. pelagica*). Partly, this is a methodological effect: since quantile regression requires a large sample size, species observed in less than 10 % of the samples were not considered. Therefore, species, specialised to specific conditions, are probably not retained for the analysis. Our findings thus underline the view that at least the most prevalent benthic species are not restricted to a single type of sediment, even if they show preference for certain sediments over others (Armonies, 2021; Snelgrove and Butman, 1994).

Furthermore, we observed differential mud tolerance between sand- and mud preferring taxa. Sand-preferring taxa were less tolerant to variations in mud content. These findings correspond with Robertson et al. (2015), who found that taxa with a preference for low mud content were generally more specialised in terms of sediment composition. This could have several explanations. Mud content is generally more variable in muddy areas than in sandy habitats (Colina et al., 2022). Besides, living in mud requires certain adaptations, such as tolerance to anoxic stress and mechanisms to separate fine sediment particles from food (Robertson et al., 2015; Snelgrove and Butman, 1994). This means that organisms inhabiting muddy habitats need these specific adaptations and need to tolerate a variable sediment composition, whereas organisms living predominantly in sand might lack the biological adaptations to tolerate mud.

Other studies have presented benthos-sediment relations in the context of functional traits. In many studies, a shift is documented from small, short lived, deposit feeders in muddy sediments to large, long-lived suspension feeders in sandy sediments (amongst others, Gusmao et al., 2022; Rhoads and Young, 1970; van der Wal et al., 2017). Although we did not focus on traits in this study, the species order we found along the sediment gradient does not underline this transition. On the contrary, suspension feeders (e.g., *C. edule*, *M. balthica*, *E. leei* and *L. conchilega*) preferred intermediate to muddy sediment and had relatively wide tolerance ranges for mud (>45 % mud). Due to the tidal currents in this dynamic system, areas with coarser sediment are not necessarily less turbid than muddy areas, meaning that they are not always more suitable for suspension feeding. Besides, some of these suspension feeders (e.g. *M. balthica*) are also facultative surface deposit feeders, utilising the microphytobenthos in muddy areas (Christianen et al., 2017).

4.3. Spatially clustered mismatches between community preference and observed sediment

In the subtidal, the actual sediment distribution generally matched the preferences of the resident species. In contrast, in the intertidal, the sediment characteristics are often coarser than the optimal sediment of the community. It appears that the few fine-grained intertidal sites provide optimal conditions, and species reach high densities, so that these sites shape the sediment optima. At the more prevalent sandier sites, the species are still present, but do not reach the optimal density or biomass. It has been shown that non-trophic interactions, such as facilitation, can enhance abundances in muddy sediment. For instance, small worms such as *H. filiformis* can oxygenate muddy sediments, increasing the inhabitable depth of the sediment (Van Colen et al., 2008), and cockles (*C. edule*) can promote microphytobenthos growth, increasing food availability for other species (Eriksson et al., 2017). Alternatively, facilitation may ameliorate conditions in sandy sediments (Bruno et al., 2003). This could hypothetically widen the tolerance range towards coarse sediments, while not shifting the optimum, if individual densities remain low. Spatially, the mismatch between optimal and realised sediment habitats was most evident at intertidal, coarse-grained stations. Furthermore, we identified clusters of stations where many species occur beyond their optimal sediment envelope. Such locations are usually found at the tidal flats beneath the head and tail of islands bordering the basin on the northern side. The discrepancies were not clearly linked to a few specific species.

A causal link of the above patterns with the 2018 ebb-tidal delta sand nourishment cannot be made, as we observed no change in Δ_{d50}, Δ_{mud} or sediment composition before and after the nourishment. This is in line with modelled sediment pathways, which suggest that it is unlikely that nourishment sand was transported to the locations where we observe sediment mismatches (Pearson et al., 2020, 2021). The locations where sediment is almost too fine for many species are situated near the inner ends of the channels and near both the mainland and Ameland ferry harbour. Here, there might be a link with ongoing human activities, such as dredging and dumping of dredged sediments. The ferry harbours and channels are continuously dredged for navigability, after which the dredged areas are filled in with mud (Rijkswaterstaat, 2022). Next to that, disposal of the dredged deposits can lead to an additional supply of mud. However, overall, most sites in our dataset are sandier than the current community prefers. It is crucial to monitor sediment composition at locations where large portions of the community are living beyond their optimal sediment range, as here even a small shift could render the habitat unsuitable for the current benthic species.

4.4. Future risks for benthic communities through sandification

As mismatches between sediment optima and habitat were stable over the studied period, communities do not seem to be shifting away from suboptimal sediments within the studied time frame. However, the skewed mismatches (Fig. 5c and f) suggest that, if this basin was to become sandier, less ideal sediment habitat might remain for current macrozoobenthos communities. This risk is largest in the intertidal areas where the difference between optimal and realised habitat is already more pronounced. Besides the foreseen sandification, which we have focussed on here, regional "muddification" of sediments also needs to be considered. For instance, in the Wadden Sea, land subsidence due to gas drilling has resulted in regional fining of the sediment by an average 1 μm decrease of d_{50} and a 3 % increase of mud content per year (de la Barra et al., 2023). Given the observed wide tolerance ranges from mud-preferring species, this will likely not result quickly in a community shift. However, such sediment fining should be monitored, especially in areas where species are already living on the edge of their mud tolerance range.

In addition to sand nourishments directly on or in front of a sandy coast, sediment nourishments could be a means to conserve intertidal habitats. Although nourishments are a highly artificial measure, they can supply sediment to prevent loss of ecosystem values when tidal flats drown due to natural and human-induced dynamics (Kabat et al., 2012). However, they should be planned and implemented carefully. Several pilot nourishments aimed at restoring tidal flats have already been performed (van der Werf et al., 2015, 2019; Escaravage et al., 2024). Benthic communities at these nourished sites did not recover to reference levels during the monitored time, partly due to the layer thickness and coarse grain size used for the nourishments. Future nourishments using finer grains (e.g. Baptist et al. (2019)) might recreate a more suitable habitat for the native benthic community. The findings of our study regarding sediment sensitivity could aid in the design when engineering natural habitats.

On a global scale, coastal sediments are subject to changes in hydrodynamics and depositional regimes due to sea level rise, changes in storm frequency and intensity, and alterations of sediment supply which might result in sandification. How coastal ecosystems will respond to this foreseen sandification depends on the sensitivity of communities to sediment properties such as grain size and mud content. The tools applied in this study aid in quantifying species and community sediment sensitivity, and can help to identify sensitive areas, where a change in sediment composition might further push the community outside of its preferred sediment habitat. Sensitivity maps as presented here could be used in combination with modelled sediment transport and composition, to predict future habitat suitability for benthic communities.

5. Conclusion

In this research, we revealed sediment preferences of macrozoobenthos, and the potential sensitivity to coarsening, "sandification", of coastal sediments. In our study area, the Borndiep, a tidal basin in the Dutch Wadden Sea, most of the studied macrozoobenthic taxa were sediment generalists, i.e., had a wide sediment preference range. Taxa that preferred coarse sediment, had narrower tolerance ranges than mud-preferring taxa. On community level, we observed a mismatch

between actual sediment composition and the preferred sediment characteristics of the resident species. Sediments were in general coarser and contained less mud than expected based on weighted mean preferences, and this difference was more pronounced in intertidal than in subtidal areas. The tools applied in this study can highlight the ecological risks of sediment change and aid in assessing the potential impacts of sandification due to coastal engineering projects and sea level rise on coastal benthic communities.

CRediT authorship contribution statement

Tjitske J. Kooistra: Writing – review & editing, Writing – original draft, Visualization, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Rob Witbaard:** Writing – review & editing, Validation, Supervision, Project administration, Funding acquisition, Conceptualization. **Tjeerd J. Bouma:** Writing – review & editing, Validation, Supervision, Conceptualization. **Stuart G. Pearson:** Writing – review & editing, Supervision, Funding acquisition, Data curation, Conceptualization. **Allert I. Bijleveld:** Writing – review & editing, Validation, Funding acquisition, Data curation. **Tjisse van der Heide:** Writing – review & editing, Validation, Funding acquisition, Data curation. **Oscar Franken:** Writing – review & editing, Validation, Data curation. **Karline Soetaert:** Writing – review & editing, Validation, Supervision, Software, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2025.109303.

Data availability

Data and R code used in this study are available at https://doi.org/10.25850/nioz/7b.b.gj.

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