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The geomorphology of an ebb-tidal-delta linked to benthic species distribution and functionality

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ABSTRACT

As a response to climate change and sea-level rise, new nourishment strategies for low-lying sandy coasts are developed. These interventions affect the habitat quality of coastal ecosystems for benthic communities. Unraveling the relationship between benthic fauna and their environment facilitates the design of sustainable management strategies for the coastal ecosystem. At the ebb-tidal delta of Ameland, The Netherlands, a unique dataset of 166 benthic and sediment samples is collected and allowed for an investigation of the macrobenthic fauna distribution at the spatial scale of morphological features. The benthic community at the ebb tidal delta is composed of species capable of withstanding the dynamic nature of these sandy coastal ecosystems. Despite the dynamic environment, the geomorphology of the ebb-tidal delta is reflected in the benthic species distribution. Distinct species assemblages were identified, covering a gradient of physical stress from extremely exposed to waves or currents, to relatively low energetic environments such as found on the delta plane seaward of the ebb-tidal delta terminal lobe. This gradient is reflected in the median grain size, organic matter content, and oxygenation of the sediment. A second gradient distinguishes well-sorted, mainly wave-exposed sediments from less well-sorted, mainly current-exposed sites. The functional characteristics of the benthic fauna show a clear contrast between the three most exposed, and the three most sheltered assemblages. Small, short-lived, surface deposit-feeding, highly mobile, burrowing organisms dominate in the most exposed sites, whereas with increasing shelter also larger, long-lived, filter-feeding and sessile organisms become more dominant. The functional characteristics suggest that the fauna of the most exposed sites will likely show a fast recovery of disturbance by sand nourishments. A much longer-lasting effect can be expected on sheltered parts of the ebb-tidal delta.

1. Introduction

Ebb-tidal deltas are shallow sandy environments at the seaward side of coastal inlet systems connecting the open sea with a back-barrier basin. The sand is transported across the ebb-tidal deltas towards the inlet by waves and transported offshore by tidal currents (Oertel, 1985). The resulting geometry of the ebb-tidal delta is controlled by the interaction of offshore tidal currents, tidal currents through the inlets, and waves (Sha and de Boer, 1991). Many ebb-tidal deltas show a pseudo-cyclic behavior over several years where the main ebb channel migrates towards the down drift barrier and shoals attach to the down drift coast, while sand is accumulated on the up drift side of the ebb-tidal delta until a new, more efficient channel is formed (Fitzgerald, 1996). Apart from the physical interactions, human interventions also influence the behavior of tidal inlets (Elias, 2006). Together this results in a dynamic and diverse coastal ecosystem with many gradients in water depth, sediment composition, wave impact, and a variety of morphological features such as shoals, migrating tidal channels and deeper waters.

In sandy ecosystems, macrobenthic species play a central role in several ecosystem services (Snelgrove, 1999). Macrobenthic species recycle nutrients, decompose organic matter, regulate nutrient cycles, redistribute sediments and organic matter through their feeding and mixing activities, and are an important food source to many species

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including humans (Reise, 2002; Snelgrove, 1999). Macrobenthos can alter the bed by filtering particles out of the water column, burrowing, building tubes, reworking the sediment, or binding sediment through mucous excretion (Reise, 2002; Widdows and Brinsley, 2002). This may stabilize or destabilize the sediment and affect sediment-water fluxes of particles, nutrients, and oxygen (Reise, 2002; Snelgrove, 1999; Widdows and Brinsley, 2002). Many of the actions leading to ecosystem-scale effects in terms of sediment stability or biogeochemical fluxes relate to fundamental physiological needs (feeding, shelter, reproduction) and life-history strategies of the species. Describing the composition of these coastal ecosystems, in terms of species or ecological traits, provides a basis for understanding the system and assessing the influence of human activities.

Most benthic organisms in sandy ecosystems are sessile or have only limited mobility within sediments (Snelgrove, 1999). As a result, many benthic species completely rely on the sediment for habitat and oxygen, and the water above them for food supply (Snelgrove, 1999). It is generally accepted that the distribution of species in marine soft-sediment ecosystems depends on temperature, salinity, and depth mainly due to physiological constraints of the species (Reise, 2002; Snelgrove, 1999). Together with sediment type and the general hydrodynamic conditions, these are the abiotic variables known to be related to the large-scale species distribution (Künitzer et al., 1992; Reiss et al., 2010; Thrush et al., 2005). On a more local scale, near-bed flow processes, bed patterns, and sediment dynamics become important, as has been documented for shallow near-shore zones (de Jong et al., 2015; Degraer et al., 2003; van Hoey et al., 2004) and estuaries (van der Wal et al., 2017; Ysebaert and Herman, 2002). Offshore bed patterns defined as tidal ridges and sand wave systems have several morphological units (e.g. troughs and crests) harboring different communities (Baptist et al., 2006; Damveld et al., 2018; Kröncke et al., 2018; Markert et al., 2015; van Dijk et al., 2012). A similar adaptation of benthic species composition to morphological features, in particular the crests and troughs of nearshore sand bars, has been described recently (Holzhauer et al., 2020).

In comparison to the relatively linear bar system of the nearshore (i.e. most prominent depth gradients in two dimensions), the ebb-tidal delta is an equally dynamic environment, but with spatially much more complicated geomorphology. Ebb-tidal deltas are curved systems with a large seaward protruding sand body and one or more tidal channels, shoals, and bars (Oertel, 1985; Sha and van den Berg, 1993) forming complex three-dimensional systems. The knowledge of how benthic species relate to the geomorphology in such a complex environment as an ebb-tidal delta is very limited.

Within this paper, the focus is on the ebb-tidal delta of the Ameland inlet between the barrier islands Terschelling and Ameland of the Wadden Sea, the Netherlands. This area has been explored as a test area for experimental coastal nourishments that supply both the North Sea coast and (indirectly) the Wadden Sea with sediment needed to withstand sea-level rise (Elias et al., 2012; Wang et al., 2018). To implement activities such as nourishments with minimal damage to the coastal ecosystem, knowledge of the processes driving benthic species distribution in such dynamic environments is needed.

For the barred system in the nearshore, Holzhauer et al. (2020) showed that although depth, sediment characteristics, and shape of the bed were important factors, the morphological features in themselves contributed most to the explanation of the species distribution. Morphological features such as bed slopes, bar crests, and troughs are an effective proxy explaining the distribution and functionality of benthic species. Here we investigate whether this holds true in the more complex environment of an ebb-tidal delta.

The species within a habitat or community can be divided into different functional types according to their mode of feeding, movement, or habit (Reise, 2002; Thrush et al., 2006; van Colen et al., 2014) where functionally similar species may be from quite different taxonomic entities (Gray, 1997). The functionality of a species within a community reflects its adaptation to the environment. Differences in the environment are reflected in the distribution of functionalities among the composing species of the community (Lavaleye et al., 2007). Consequently, we hypothesize that differences in assemblage composition and functionality will be observed across the environmental gradients and geomorphology of the ebb-tidal delta.

The aim of this paper is (1) to assess the spatial pattern of benthic communities at the ebb-tidal delta; (2) to analyze the functional types of the species within a community according to their mode of feeding, movement, or habit and (3) to relate the distribution of benthic species to the geomorphology of the ebb-tidal delta. Our study is based on detailed descriptions of the Ameland ebb-tidal delta and its benthic fauna, yet the conclusions are generalized to this type of coastal system elsewhere by emphasizing the relation between geomorphology and environmental gradients, and the ecological traits characterizing the benthic community.

2. Materials and methods

2.1. Description of the study area

The ebb-tidal delta of Ameland is a mixed-energy inlet, located between the barrier Islands Terschelling and Ameland in the Netherlands, where tides and wind-generated waves are the dominant processes governing morphological development and sediment transport (Fig. 1). The water flow through the inlet is mainly driven by a semi-diurnal tide with an average amplitude of 0.77 m. Due to shallow water effects, there is a significant asymmetry with a faster rise than fall of the tide and considerable influence of the spring-neap tidal cycle. This can result in an increase in the tidal range to 3 m during spring-tide (Elias et al., 2019).The mainland shelters the Ameland inlet from the strongest and most frequent winds occurring from the southwest, causing the dominant wave direction and wind direction not to be aligned. The overall wave climate is mild, with significant wave heights below 2 m and most waves coming from directions between north-northwest and east (Elias et al., 2019).

The Ameland ebb-tidal delta, with its complex shoals and channels, shows strong gradients in depth over a relatively small spatial scale (Fig. 1). There is a deep main ebb channel, the “Borndiep”, with parts that exceed 25 m in depth and steep slopes. Next to this channel, a smaller channel system connected to the “Westgat-channel” (approx. 7–10 m water depth) is present. On the ebb-tidal delta itself, the “Akkepollegat” is the largest channel. In the past, it had a pronounced seaward outflow where only recently two ebb chutes have formed. The “Kroftmansbult” is one of these ebb chutes covering now most of the shoal area. This shoal is shallow with water depths between 1 and 2 m. The eastward migration of this shoal has distorted the outflow of “Akkepollegat” and pushed the channel eastwards (Elias et al., 2019). Northeast of the “Akkepollegat” a large shallow swash platform named “Bornrif” separated from the coast by a small channel is present. In the north, this platform has several bars migrating towards the coast (Brakenhoff et al., 2017). In the center, the platform is very shallow without bars. Seaward of the terminal lobe of the ebb-tidal delta, a deeper plane is present, the “Vlakte van Ameland”.

The sediment consists of fine sand (125–250 μm) with medium sand (250–500 μm) in the main channel (Borndiep). The mud content (<63 μm) is the highest in the northeast at the margins of the ebb-tidal delta (Elias et al., 2019).

2.2. Classification of the ebb tidal delta into physiotopes

Preceding the field campaign, physiotopes were defined based on environmental parameters following the concept of morphological features described by Holzhauer et al. (2020). A physiotope is a collection of physical characteristics or features that distinguish different areas. For the ebb-tidal delta, we selected the terrain parameters bed level,

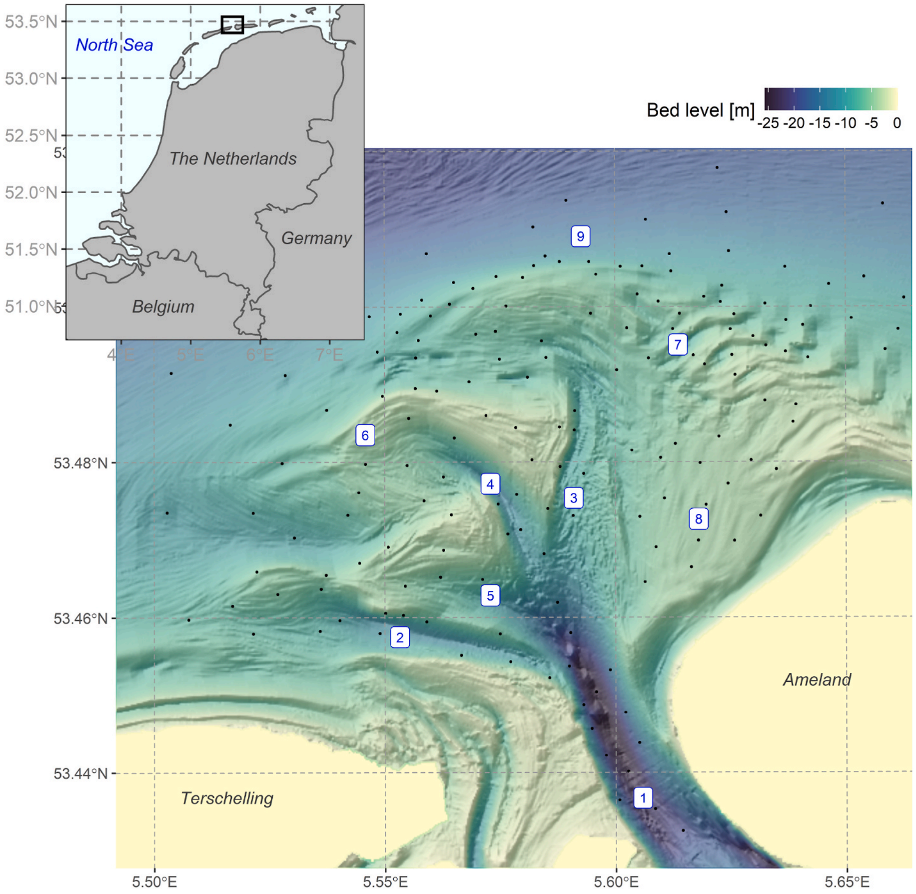


Fig. 1. Channels and shoals of the Ameland ebb-tidal delta in 2017, depth contours (source: Rijkswaterstaat). Bed level is measured with respect to NAP (Normaal Amsterdams Peil), approximately mean sea level. 1) Borndiep, 2) Westgat, 3) Akkepollegat, 4) ebb chute-1, 5) ebb chute-2, 6) Kroftmansbult 7), Bornrif platform, 8) Shallow center of the Bornrif platform, 9) Vlakte van Ameland bordering the terminal lobe. The sampled locations are indicated by black dots.

slope and orientation of the bed, and bed level change within one year to translate the geomorphology of the ebb-tidal delta into homogenous morphological features with a distinct abiotic character. The slope of the bed distinguishes between flat and steep. The orientation of the bed influences the exposure or shelter to waves and currents (Wilson et al., 2007) which determine disturbance of the bed and also transport of (pelagic) food to the benthic fauna. The sedimentation rate over one year is presumed to influence the survival, settling, and feeding strategy of benthic species (Mestdagh et al., 2018). The terrain parameters were derived from bathymetric maps, with a 20 × 20 m grid size, collected by the Ministry of Public works and Infrastructure in the summer of 2016 and 2017. The slope and orientation of the bed were obtained using the Fleming and Hoffer algorithm for smooth surfaces (Fleming and Hoffer, 1979), and the yearly bed level change by subtracting the 2017 and 2016 bathymetry. A k-means classification procedure without spatial limitations within the ArcGIS 10.4.1 package was used to group the terrain parameters and construct homogenous morphological features. This allowed for a definition of areas defined by a combination of input parameters rather than a ranked sequence of classifications based on the input parameters. The optimal number of morphological features was selected using the pseudo-F-statistic of Calinski-Harabasz (Calinski and Harabasz, 1974).

Sediment composition and hydrodynamic conditions are, next to the terrain parameters, important drivers structuring the benthic species distribution (Degraer et al., 2003; van Hoey et al., 2004; Ysebaert and Herman, 2002). Recent datasets for these parameters were not available and therefore excluded from the k-means classification. In a subsequent step, sediment composition measured in 2001 (TNO, 2017), and the energetic conditions described by the spatial variation in the maximum bed shear stress over the ebb delta based on output from existing Delft3D model simulations of the Ameland inlet during both ebb and flood conditions (De Fockert, 2008; Elias et al., 2015; Wang et al., 2016), were used to refine the morphological features. A subdivision between medium coarse and medium fine sand was created. The subdivision in energetic conditions is described with three classes each relative to the mean maximum bed shear stress; areas with relatively low (<25th percentile), average (25–50th percentile) and high (>50th percentile) energetic conditions.

Finally, smoothing was used to divide the ebb-tidal delta landscape into clearly distinguishable, spatially smooth areas, which we called physiotopes. These physiotopes formed the framework for the sampling of sediment and benthic fauna in the field.

2.3. Fieldwork and sample handling

In September 2017, a total of 166 samples were collected at the ebb-tidal delta of Ameland (van Prooijen et al., 2020). Stratified random samples were taken with a box-core (sample surface 0,1 m^2 and penetration depth between 15 cm and 30 cm) within the predefined physiotopes. An alternative strategy of sampling the entire area on a regular grid was rejected as it could have resulted in missing small physiotopes (Legendre et al., 2002).

The apparent Redox Potential Discontinuity (aRPD) was visually derived from each box-core and used as a proxy for sediment mixing and oxygenation (Rhoads and Germano, 1982). The distance from the top of the intact sediment core to the point where the light brown or light grey oxic sediment turns into a darker grey of black suboxic or anoxic sediment was measured.

Sediment subsamples of the upper 8 cm of the box-core were taken and directly frozen for analysis of sediment composition and organic matter. The remaining material was wet sieved over a 1 mm mesh size sieve to extract the macrobenthic species. The retained matter was collected, fixed with 4–6% neutralized formaldehyde and stained with Bengal-rose to be analyzed in the laboratory.

Each species was identified to the lowest practical taxonomic level and counted. Ringworms (*Nemertea*) were not specified into species and for hard substrate species (Bryozoa and Cnidaria species) only presence-absence was recorded (Verduin and Leewis, 2018). Organic matter was analyzed by loss on ignition at 550 °C. The sediment grain-size distribution was analyzed with laser diffraction (Malvern Master-sizer) at the University of Gent. To analyze the sediment particles as they were present in the bed and available to the benthic species, the sediment samples were not cleared from organic material or carbon parts. Grain size fractions were derived as volume percentages according to the Wentworth scale mud (<63μm) to very coarse sand (1–2 mm). All data is permanently stored at the 4TU.Center for Research Data (Rijkswaterstaat and Deltares, 2019).

2.4. Data analysis

For each sample the sediment characteristics sorting, skewness and kurtosis were calculated (Folk and Ward, 1957).

Soft substrate species found in more than four locations (approx. 2% of all samples taken) were included in the analysis. Rare species were first grouped at the genus level. This resulted in 44 out of 102 taxa being utilized in the analysis. Regarding all taxa found, the selected taxa contained 99% of the total abundance and had a similar relative abundance within the different phyla. One location recorded zero species.

The community structure of the benthic fauna was investigated followed by functional characterization of the benthic communities and finally linked to the dynamic condition of the ebb-tidal delta. The data were explored and checked for outliers, normality, and collinearity (Zuur et al., 2010). For each location, univariate statistics such as species density (D), species number (S_n), and species diversity expressed as the Shannon diversity index (H′) and Simpson diversity (D_s) were calculated. Shannon's index accounts for both the abundance and evenness of the species present at a location, whereas the Simpson-index is less sensitive to rare species.

Assemblages were identified based on species abundance using cluster analysis, with chord distances and Ward's minimum variance method (Borcard et al., 2011; Legendre and Legendre, 1998; Murtagh and Legendre, 2011). To down weight the importance of very abundant species, the species abundance data were fourth-root transformed. The relationship between the assemblages was visualized in a non-metric Multidimensional Scaling (nMDS) plot based on the same fourth-root transformed abundance data.

The benthic assemblages found were characterized by means of species number, density, diversity, functionality, indicator species, and dominant species. Non-parametric multivariate analysis of variance was used to test whether the assemblages differed for the environmental parameters and species characteristics. When the results were significant ($p < 0.05$), post hoc Tukey-HSD tests were used to explore which assemblages differed. Niche breadths varies among species, implying that a species can be associated with one or more assemblages. Indicator species analysis undertaken on single assemblages may fail to reveal this association of species to multiple assemblages (De Cáceres et al., 2010). Allowing species to associate with multiple assemblages enabled us to distinguish those species that characterize a single assemblage from those that characterize the relationships between assemblages. Therefore indicator species were calculated for single assemblages and combinations of assemblages. A species was identified as indicator species for a specific assemblage when the predicted value restricted to the assemblage for this species was above 70% and the species appeared in more than 50% of the sites related to the assemblage.

The functionality of species within an assemblage was investigated by analyzing basic biological traits and the functionality of the species present. Biological traits and their modalities for each species were derived from the consultation of several online trait-datasets (BIOTIC, PolyTraits, Worms), literature (Bos et al., 2011; Fauchald and Jumars, 1979; Holtmann et al., 1996; Jumars et al., 2015; Marine Ecological Surveys Limited, 2008; McHugh and Fong, 2002; Queirós et al., 2013; Van Der Linden et al., 2012) and consultation of experts. Traits concerning life history (Size, Life span, Reproduction frequency, Reproduction age), habit and behavior (Feeding mode, Mobility type), and ecosystem engineering (Bioturbation) were included (Table 1). The trait Mobility type is a combination of the traits Movement, Mobility, and

Table 1
Selected traits representing Life history, Habit and behavior, and Ecosystem engineering function of the species with their modalities. The trait Mobility type is a combination of the traits Movement, Mobility, and Habit.

Life history **Size**	**Life span**	**Reproduction frequency**	**Reproduction age**
<1 cm	<1 year	seasonal yearly	<1 year
1–3 cm	1–3 years	continuous yearly	1–2 years
3–10 cm	3–5 years	twice yearly	2–3 years
10–15 cm	5–10 years	semelparous	3–5 years
>15 cm	10–20 years	not known	not known

Habit and behavior **Feeding mode**	**Mobility type**
sub-surface deposit	burrow dwelling; a burrowing species with a habit of dwelling in the burrow
surface deposit	burrowing; a burrowing species living free in the sediment with limited mobile mobility
suspension feeder	crawling; a crawling species living free in or on the sediment with limited to mobile mobility
omnivore	sessile; a burrowing species with a habit to remain mostly at one place in the sediment
predator	tube-dwelling; a tube building species with a habit to dwell in its tube

Ecosystem engineering **Bioturbation**
surficial modifier
up/downward conveyor
upward conveyor
downward conveyor
bio-diffuser

Habit. Bioturbation classifies the ability of species to alter and engineer their environment. Each species can exhibit several modes within the behavioral or ecosystem engineering traits. Only the mode exhibited predominantly was selected.

To determine which species and environmental parameters drove the separation of the benthic communities, the nMDS-ordination was correlated to species and environmental parameters with the use of a permutation test (perm = 999). Non-collinear environmental parameters were selected based on variance inflation factors and collinearity (Appendix Table C.1). All analyses and figures were performed in R-4.0.2 (R core team, 2020) and the additional packages vegan-2.5-6, tidyverse-1.3.0, patchwork-1.0.1, raster-3.3-7, sf, rnaturalearth-0.1.0, and indicspecies-1.7.9.

3. Results

3.1. The geomorphology of the ebb-tidal delta expressed in physiotopes

For the Ameland ebb-tidal delta the k-means classification identified eight main physiotopes. The refinement based on both the global sediment composition in 2001 and expected energetic conditions based on the output from existing Delft3D model simulations resulted in 1) a division along the Akkepollegat channel with medium coarse sand at the west side and medium fine sand at the east side and 2) a division between the dynamic shoals and outer rim of the ebb tidal delta, the more stable Bornriff platform, and the deeper channels. The latter corresponds with the conceptual description of the morphodynamic behavior of the ebb-tidal delta by Elias et al., (this issue). This resulted in a subdivision of the main physiotopes at the eastern and western flank, with high sedimentation or erosion rates, at the sloping bed, and in the channels (Table 2 and Fig. 2).

3.2. The general characteristics of the ebb-tidal delta

3.2.1. Sediment characteristics

The sediment at the ebb-tidal delta in 2017 consisted of homogenous (skewness: 87% symmetric, 9% very fine-skew and, 4% fine-skew), well-sorted (84% of the locations) medium sand (D_{50} 212 ± 30 μm). The organic matter content (OM) was low and ranged between 0.25 and 1.3%. The spatial distribution of the median grain size showed finer sediment in the east and north-east of the ebb-tidal delta (Fig. 3-A). Here a small part of the locations (6%) consisted of moderately sorted fine sand with a very fine skew and an organic matter content ranging between 0.5 and 1% (Fig. 3-B and C). Little coarser well-sorted sand with an organic matter content between 0.25 and 0.5% was found in the west on the ebb-shields of the ebb-tidal delta. In the main channel, some locations (4%) were poorly sorted and consisted of fine sand to medium sand with a very fine skew and an organic matter content ranging between 0.75 and 1.25%. The bed level changes over one year were the largest at the shoals and the north of the Bornrif (Table 2). This is reflected in the aRPD, with no visual aRPD at these locations and an aRPD of 15–20 cm at the shallow center of the Bornrif swash platform and 5–15 cm at the northeastern part of the ebb-tidal delta (Fig. 3-D).

3.2.2. Species diversity and functionality at the ebb-tidal delta

At the ebb-tidal delta 82 unique species and 20 higher level taxa were found. A small percentage (3.7%) of the organisms were juveniles. In soft-sediment, a single grab covering only 0.1 m^2 of the bed, is known to sample only a fraction of the species at a location because of small-scale spatial variation. The true species richness estimated at 116 ± 19 species indicated that around 88% of the expected species were collected (non-parametric Chao2-method (Chao, 1987; Colwell and Coddington, 1994)).

Arthropoda formed the most dominant taxonomic group followed by Annelida and Mollusca. The number of species within one location ranged between 0 and 23 species with an average number of 9 ± 5 species. The highest number of species was found in the northeast of the ebb-tidal delta and the lowest in the channels (Fig. 4-A). The species *Nephthys cirrosa*, *Magelona mirabilis*, *Magelona johnstoni*, *Pontocrates altamarinus*, *Bathyporeia elegans,* and *Spio martinensis* were found in more than 50% of the locations sampled. The most common species was the bristle worm *Nephthys cirrosa*, found in 81% of the sampled locations.

The total species abundance is dominated by the sand digger shrimp, *Bathyporeia pelagica (16% of total abundance)*. The species *Bathyporeia pelagica, Urothoe poseidonis*, *Magelona johnstoni*, *Bathyporeia elegans,* and *Ensis* were the most abundant species and together encompassed 50% of all organisms found. The total abundance at a single sample location ranged between 27 and 2787 ind/m^2 (Fig. 4-D). The highest abundance was found at the delta plane seaward of the terminal lobe and the southern part of the ebb shields. At the delta plane, mainly high densities of Annelida and some Mollusca were found while, at the ebb shields the high species abundance is mainly caused by Arthropoda only (Fig. 4-D). The Shannon-index ranged between 0.3 and 2.8 with the highest values at the delta plane, indicating a higher species diversity (Fig. 4-B). The Simpson-index ranged between 0.1 and 0.9 with the highest values spread over the entire ebb-tidal delta, indicating that the most dominant species were evenly spread over the ebb-tidal delta (Fig. 4-C).

The macrobenthic species were generally very small (<1 cm; 45% of all individuals found) to small-medium sized (3–10 cm; 30%). Most species had a life span shorter than one year (50% of all individuals found) followed by species with a life span of 3–5 years (31%). Seven percent of the species had a life span of 10–20 years. The life span corresponded with a fast reproduction age (<1 year; 57%) and a high reproduction frequency (Yearly; 37% and continuous; 35%). Surface deposit-feeding was the most important feeding mode (70%), followed by suspension-feeding (16%), predation (9%), and sub-surface deposit feeding (4%). One percent of the individuals consisted of omnivore species. The general mobility type was burrowing (64%) followed by sessile (19%), tube-dwelling (10%), burrow-dwelling (4%), and crawling (3%) species. Most species found at the ebb-tidal delta only altered their environment in a surficial way (77%). Some species were able to transport sediment in the bed both up and down (Upward/downward conveyor; 10%), others moved sediment in random directions over short distances (bio-diffuser; 9%). Only a very small percentage of the species moved sediment into one direction, upward (Upward conveyor; 3%), or downward (downward conveyor; 1%).

3.3. Species assemblages of the ebb tidal delta

With hierarchical cluster analysis, six assemblages of benthic species were identified (Ward's distance at 2.4 minimal within cluster variance) (Fig. 5-A). These benthic species assemblages all included sample stations that belonged to several of the predefined physiotopes (Figs. 2 and 5-B). Generally, the *Offshore* and *Flank-east* physiotopes were covered by assemblage A. The physiotopes *Flat-shallow* and to a lesser extent *Channel Inlet* with *Slope-Borndiep* spanned respectively, assemblage C and E. These assemblages showed the best linkage with the predefined physiotopes. For the more dynamic shoals, several physiotopes were defined with different sedimentation-erosion patterns and slopes of the bed. There were no assemblages with a clear link to these physiotopes. Nevertheless, the assemblages did show a division in locations at the top of the shoal (assemblage E) and the ebb-chutes of the shoal (assemblage D). Assemblage B occurred along the contours of the ebb-tidal delta and spanned parts of several physiotopes among which *Flank-west*, *Channel-Bar* and *Erosion-Bornrif* (Appendix, Table B.1).

Table 2
Description of the physiotopes with the number of randomly taken samples (#samp).

	Habitat	Description	#samp
1	Offshore (O)	Fairly gentle slope (0.33 ± 0.16 deg), oriented north (N 81% and NW 19% of the habitat area) with little bed level changes over the year (−0.02 ± 0.08 m) located seaward the terminal lobe with water depths of 15.2 ± 1.8 m.	11
2a	Flank-East-Shallow (FES)	East flank of the ETD with a north-north-eastern orientation (N 60% and NE 31%). The slope is gentle (0.21 ± 0.08 deg) with almost no bed level change (0.00 ± 0.16 m) and a water depth of 7.2 ± 0.5 m.	6
2 b	Flank-East-Deep (FED)	East flank of the ETD with a northern orientation (N 98%) with almost no bed level change within a year (0.08 ± 0.12 m). Compared to FES the area is deeper (water depth 9.9 ± 1.2 m) with a steeper slope (0.46 ± 0.26 deg).	6
3a	Flank-West-Shallow (FWS)	West flank of the ETD with a bed orientation varying between northwest and southwest (N 25%, NW 25%, SW 13%, S 19%). The slope is gentle (0.23 ± 0.18 deg) with almost no bed level change (0.03 ± 0.16 m) and a water depth of 7.0 ± 0.6 m.	6
3 b	Flank-West-Deep (FWD)	West flank of the ETD with a northwestern orientation (NW 53%, N 18%, SW 11%) with almost no bed level change within a year (0.03 ± 0.09 m) and a gentle slope (0.20 ± 0.12 deg). Compared to FWS the area is deeper (water depth 9.7 ± 1.0 m).	6
4a	Sedimentation-Bornrif (SB)	Bornrif with increased sedimentation rates (0.82 ± 0.4 m). The water depth is shallow with 5.4 ± 1.0 m and a steeper slope (0.50 ± 0.41 deg) varying in northwestern and northeastern direction (N 36%, NE 16%, NW 10%, E 9%, S 9%). Sediment is classified as medium-fine sand	11
4 b	Sedimentation-Shoal (SS)	The shoals of the ETD with a shallow water depth (5.1 ± 1.8 m) and increased sedimentation over one year (1.04 ± 0.90 m) and varying slopes (0.47 ± 0.42 deg) with orientation in each direction (N 21%, NW 21%, NE 10%, SW 10%, S 19%). Sediment is classified as medium-coarse sand.	11
5a	Erosion-Bornrif (EB)	Bornrif with a shallow water depth (5.3 ± 1.4 m) and a decrease in bed level over one year (−0.75 ± 0.48 m). The slopes are varying (0.43 ± 0.36 deg) with orientations in each direction (N 23%, NW 21%, NE 13%, W 13%, SW 12%). Sediment is classified as medium-fine sand.	11
5 b	Erosion-Shoal (ES)	The shoals of the ETD with shallow water depth (6.8 ± 3.3 m) and a decrease in bed level over one year (−0.86 ± 0.49 m). The slopes vary (0.55 ± 0.43 deg) with orientations most in southern direction (S 27%, SW 21%, SE 14%, N 12%, NE 12%). Sediment is classified as medium-coarse sand.	11
5c	Erosion-Delta front (ED)	An area at the front of the ebb-tidal delta with a water depth of 7.9 ± 1.1 m and a decrease in bed level of −0.43 ± 0.33 m over one year. The slopes are steeper (0.40 ± 0.34 deg) with most north northwestern orientation (NW 52%, N 15%, W 13%, S 10%).	11
6	Shallow flat (F)	Shallow (4.7 ± 1.3 m) and flat (0.17 ± 0.16 deg) area near the Bornrif without bed level changes over one year (0.01 ± 0.19 m). The orientation of the area is most in a western direction (W 41%, NW 20%, SW 11%)	22
7a	Slope-Shoal (SLS)	Steep slopes (2.43 ± 1.02 deg) along the shoals, a water depth of 7.1 ± 2.2 m, and large changes in bed level over one year 1.43 ± 1.82 m. The orientation of the slope is in each direction (E 31%, N 24%, S 20%, NE 13%)	15
7 b	Slope-Borndiep (SLB)	Steep slopes (2.96 ± 1.44 deg) along the Borndiep with deeper water (13.3 ± 6.1 m) and little bed level changes over the year (−0.27 ± 1.32 m). The orientation of the bed varies in each direction (NE 31%, SW 24%, N 16%, E 15%, W 12%)	11
8a	Channel-Shoal (CS)	Channels in between the shoals with a water depth of 6.7 ± 2.7 m and steeper slopes (0.46 ± 0.37 deg) with orientations both in a southerly and westerly direction (S 21%, SW 17%, W 15%, NE 11%, SE 10%). Changes in bed level over one year are small (0.28 ± 0.46 m).	11
8 b	Channel-Bar (CB)	Shallow area (5.8 ± 1.0 m) at the seaward side of the main channel with no bed level changes over the year (0.05 ± 0.21 m). The slope is gentle (0.27 ± 0.30 deg) with varying orientation in both north and southern direction (N 33%, S 23%, SW 13%, NW 9%)	11
8c	Channel-Inlet (CI)	The main channel between the barrier islands. The water depth is large (18.7 ± 4.1 m) with little bed level changes over the year (0.23 ± 0.66 m) and steeper slopes (0.80 ± 0.42 deg) with a western and eastern orientation (SW 36%, S 13%, W 13%, NE 11%, E 10%, SE 8%).	6

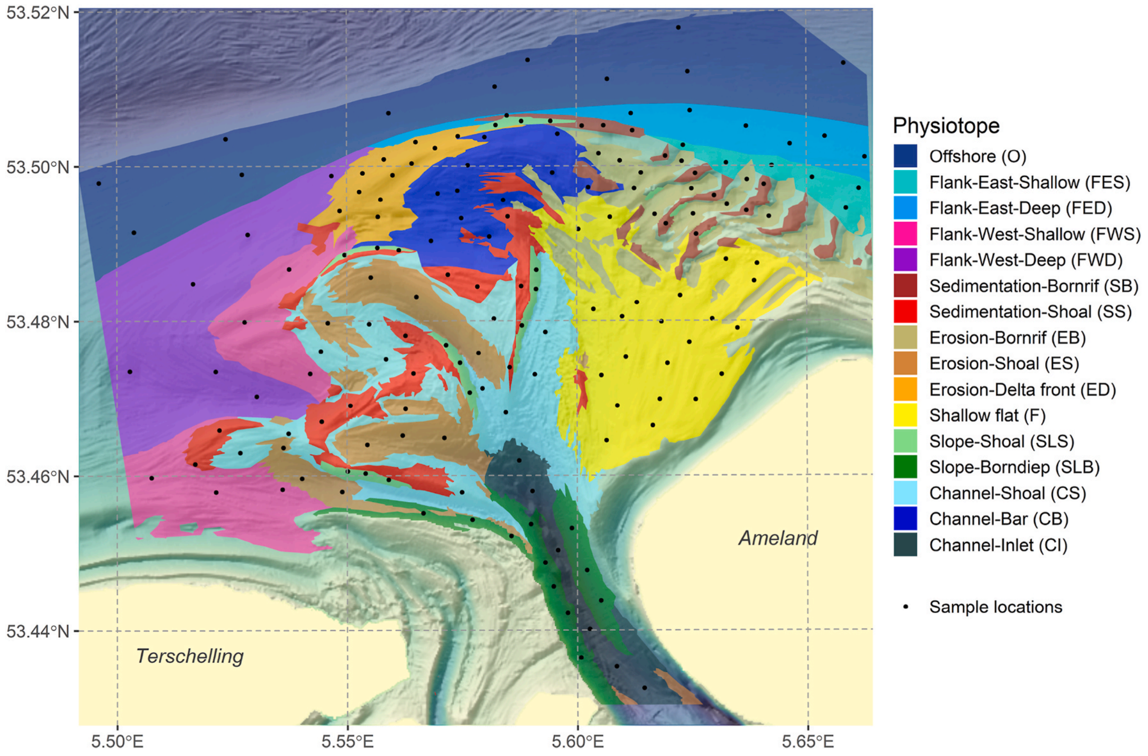


Fig. 2. Overview of the physiotopes of the Ameland ebb-tidal in 2017. The sampled locations are indicated by black dots.

3.3.1. *Species composition and indicator species*

The benthic species composition of the six assemblages differed significantly ($p < 0.001$, Permanova). Assemblage-A, the *Fabulina fabula – Lanice conchilega – Magelona* community, comprised larger species such as Mollusca and Echinodermata together with Annelida and Arthropoda species. *Urothoe poseidonis, Tellimya ferruginosa, Spisula subtruncata, Fabulina fabula, Lanice conchilega, and Nephthys hombergii* were identified as indicator-species and dominantly present (Appendix Table B.1). Within assemblage-C, the *Ensis – Magelona* - community, mostly Annelida and Mollusca were found and no indicator species were identified. The most dominant species were *Ensis* and *Magelona mirabilis*. Assemblage-B, the *Capitella – Magelona* community, did not have a clear signature, as no indicator species were found. The assemblage comprised some Mollusca but not in the numbers found in assemblages A and C. Mostly Annelida and Arthropoda were found. Indicator species were not identified and *Urothoe poseidonis* and *Magelona johnstoni* were most dominant. Most frequently found was the polychaete worm *Capitella*. Assemblage-D, the *Bathyporeia elegans – Bathyporeia pelagica* community consisted of Arthropoda and some Annelida species. Indicator species were not identified and *Bathyporeia pelagica* with *B. elegans* were dominantly present. Assemblage-E, the *Pontocratus arenarius – Bathyporeia pelagica* community, consisted mainly of Arthropoda with *Pontocrates arenarius* and *Gastrosaccus spinifer* as indicator species. *Pontocrates arenarius* together with *Bathyporeia pelagica* were dominantly present. Finally, assemblage-F, the *Haustorius arenarius* community, consisted of Annelida and Arthropoda with *Bathyporeia pelagica* as the most dominant species.

Besides the indicator species per assemblage, indicator species for combined assemblages showed a division into two groups. The first group comprised assemblage A, B, and C with *Magelona johnstoni* and *Spio martinensis* as indicator species. Within this group, the combined assemblages A and C had *Ensis, Limecola balthica,* and *Spiophanes bombyx* as indicator species and the combined assemblages A and B had *Capitella* as species indicator. A second group is composed of the assemblages found at the more dynamic part of the ebb-tidal delta, the ebb shields and channels. Here the assemblages D and E bond together with *Bathyporeia pelagica* as indicator species. *Haustorius arenarius* was found as indicator species for the bond between assemblage E and F. A final bond was found between all assemblages except assemblage-E with *Magelona mirabilis* as indicator species.

3.3.2. *Species functionality within the assemblages*

The analysis of the species functionality within the assemblages showed that surface deposit feeders were dominant in each assemblage. Suspension feeders were only found in assemblage A, B, and C, with the highest densities in assemblage-A and smallest in assemblage-B (Fig. 6). Mobility traits in the assemblages D, E, and F were dominated by burrowing species. A combination of burrowing and sessile or tube-dwelling species was found in assemblages A, B, and C. The expected life span was the largest in assemblage-A. In the more ‘dynamic’ assemblages at the ebb-shields and the channels, very few organisms belonged to species with a life expectancy exceeding three years, and most lived shorter than one year. This is reflected in the reproduction age which is mostly within one year with a continuous reproduction frequency. The largest species were found in the assemblages A and C.

3.3.3. *Community and environmental characteristics of the assemblages*

Community characteristics and environmental parameters differed significantly between the species assemblages (Permanova permutation test, $p < 0.05$) (Appendix Table A.1). For assemblage-A, all community characteristics differed significantly from the other assemblages, as assemblage-A had the highest value for the average density ($D = 1236 \pm 484\ Nm^{-2}$), both diversity indexes ($H' = 2.21 \pm 0.3$; $D_s = 0.83 \pm 0.1$) and species number ($S_n = 17 \pm 3$). The lowest species density and species number were recorded for assemblage-F ($D = 188 \pm 145$; $S_n = 5 \pm 2$), where the lowest diversity index values were found for assemblage-E ($H' = 0.94 \pm 0.3$; $D_S = 0.47 \pm 0.2$) (Fig. 7-A and Appendix Table B.1). The assemblages C and D showed no significant differences in community characteristics.

The sediment characteristics, sorting and skewness, together with the mud fraction were very similar across the assemblages, except for assemblage-A with much higher values. The values of the other

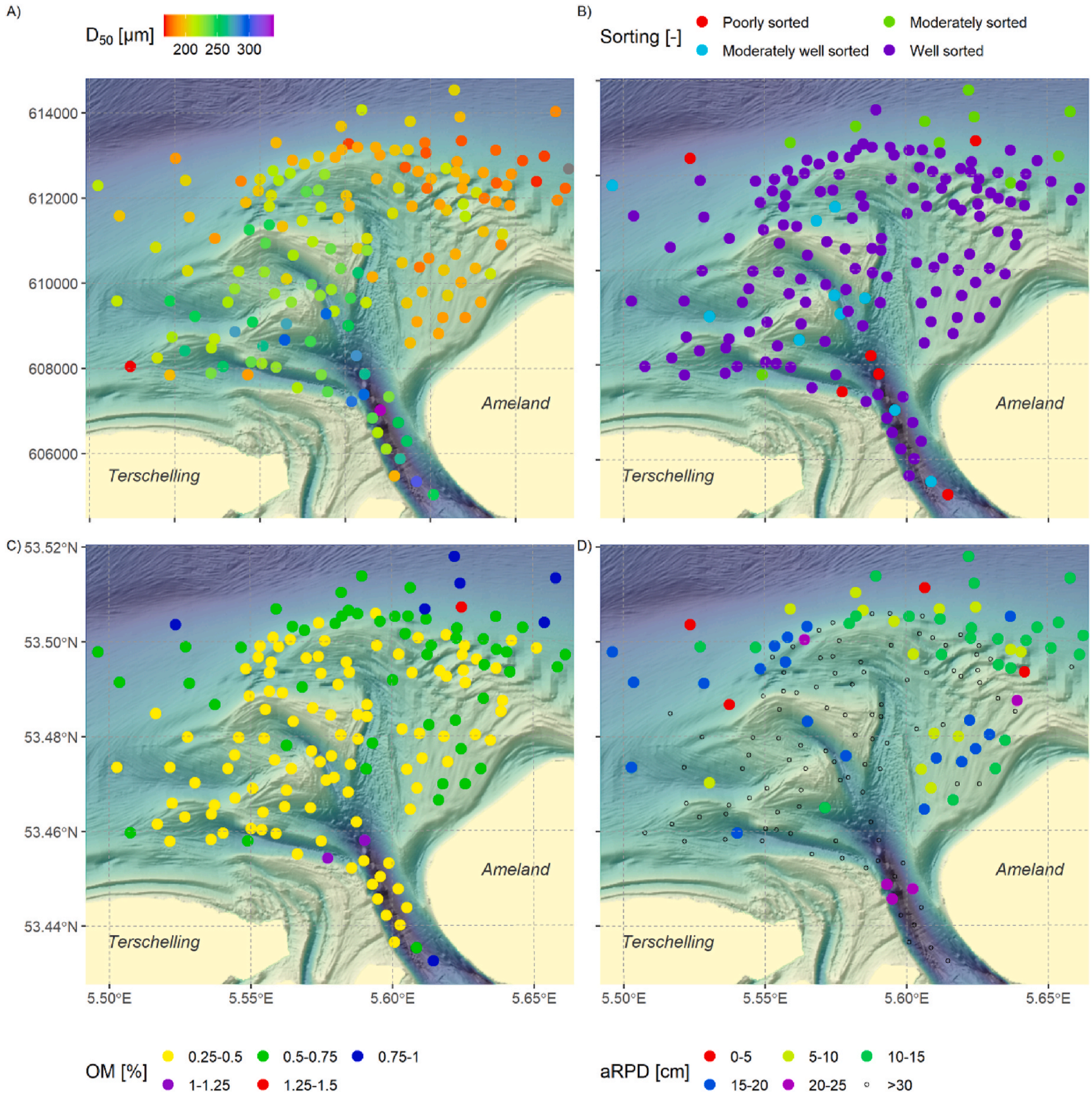


Fig. 3. Environmental parameters measured in 2017. A) Median grain size (D_{50}), B) Sediment sorting, C) Organic matter content (OM) and D) visual depth of the redox potential discontinuity (aRPD). An aRPD of more than 30 cm could not be measured due to the maximum depth of the box-core and is indicated by an open circle.

environmental parameters for grain size (D_{10}, D_{50}, D_{90}), sediment fraction (M, VFS, FS, MS CS), morphometry (slope, ΔH_{bed}), and the remaining sediment characteristics (aRPD, OM), were not systematically different between the individual assemblages either. However, differences do exist at the level of assemblage groups. The first group consisted of assemblages A, B, and C and the second group consisted of assemblages D, E, and F. Note that this is a similar division into groups of assemblages as found for the combined indicator species.

A more detailed look at this division (Appendix Tables A.1 and B.1 and Fig. 7-B-D) revealed that the first group of assemblages showed small differences in environmental parameters which were not always significant, except for bed level. Typically, bed level change (ΔH_{bed}) was around zero and the bed had a gentle slope ($<0.7^\circ$). This was reflected in an aRPD between 14±8 cm and 21 ± 10 cm and an OM-content around 0.5%. The shallowest aRPD (14±8 cm) together with the highest OM-content (0.68 ± 0.2%) was measured at assemblage-A. The grain size was approximately 20 μm smaller compared to the other group with a gradual increase from assemblage A, C to B, where assemblages A and B differed significantly from each other. The differences for each parameter within the second group were larger, except for aRPD and OM-content. The second group distinguished itself with little steeper slopes around 1°, an aRPD exceeding 30 cm, and an OM-content below 0.5%. The grain size was medium to coarse ($D_{10} > 150$ μm, $D_{50} > 220$ μm, and $D_{90} > 315$ μm) with significant differences for grain size and sediment fractions between assemblages D and E. The change in bed level (ΔH_{bed}) did not significantly differ within the group and reached a maximum of 1.24 ± 2.64 m at assemblage-E. For bed level, assemblage-F (−11.31 ± 6.4 m) differed significantly from both assemblage-E (−4.36 ± 1.4 m) and D (−5.71 ± 2.4 m). Where assemblages D and E are comparable, note that the variance for assemblage-D is twice the size of assemblage-E.

3.3.4. *Associating with environmental parameters*

The differences between the benthic species assemblages are visualized with a nMDS-ordination (Fig. 8). The species and physiotopes with the best fit to the ordination (ENVFIT $p < 0.05$) are shown.

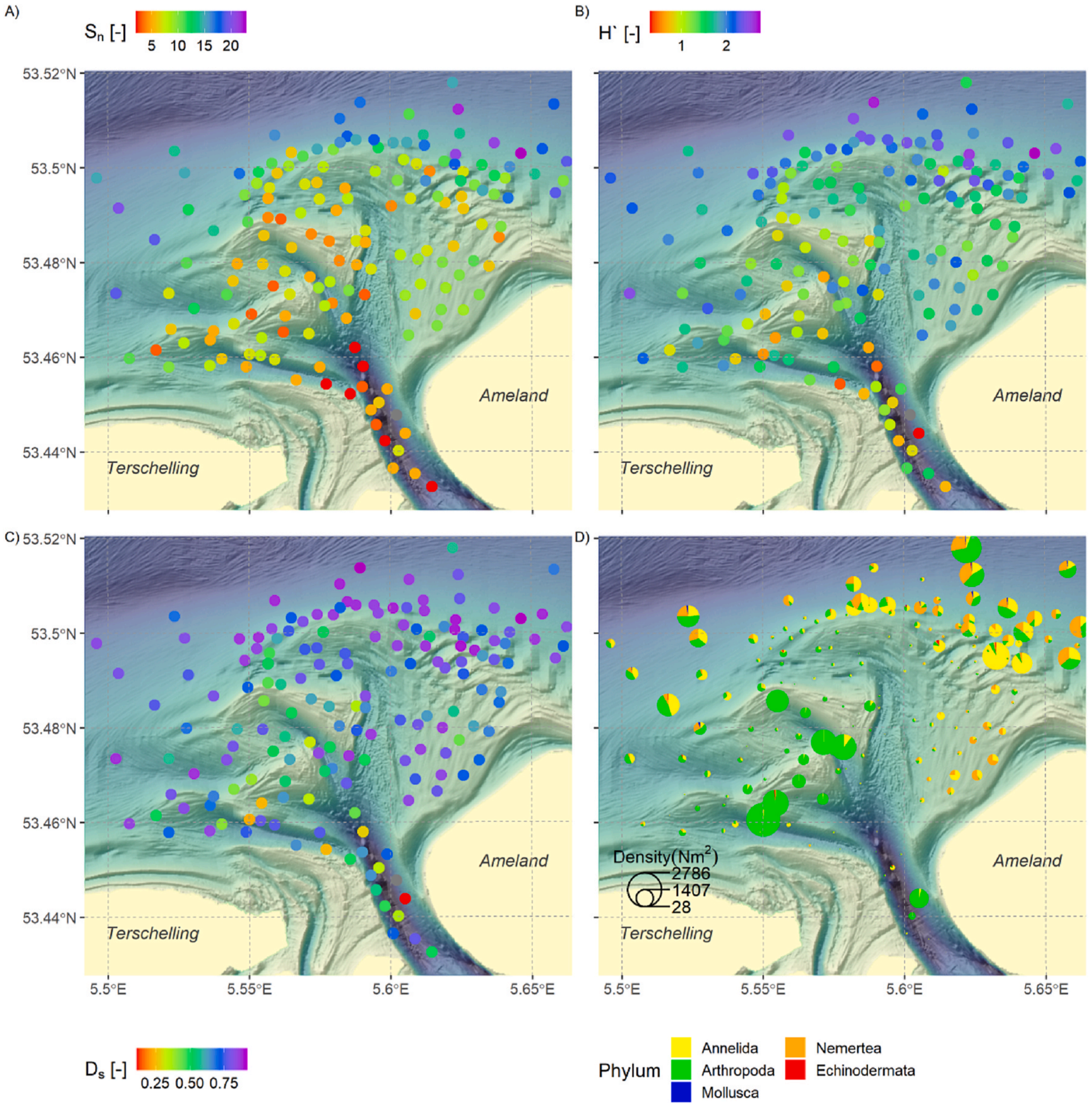


Fig. 4. Spatial distribution of species density and diversity at the ebb-tidal delta, A) the number of species (S_n), B) Shannon-Wiener diversity index (H′), C) Simpson diversity index (D_s), and D) total abundance (D) with a distinction at phylum level over the ebb-tidal delta.

Indicator species for a single assemblage (bold) and multiple assemblages (italic) are positioned close to their assemblage. This is similar for the physiotopes related to the assemblages. The parameters medium-sand and fine-sand strongly correlated (>0.8) with D_{50} and the parameters skewness, kurtosis, and mud fraction strongly correlated with sorting. The grain size D_{90} correlated with D_{50} and coarse-sand. (Appendix Table C.1).

The first nMDS-axis describes a gradient from fine, muddy, and organic-rich sediments (left) to coarser, organic-poor, and very well oxygenated sediments (right). The assemblages, except for assemblages C and F, are arranged along the first nMDS-axis. The assemblages C and F show overlap with the other assemblages along the first nMDS-axis and separate on the second nMDS-axis. For the second axis, no clear association with the environmental parameters measured was found.

4. Discussion

Ebb-tidal deltas are shallow and very dynamic areas and often not included in field monitoring campaigns, resulting in limited knowledge of the presence and role of benthic species. This study is, to the best of our knowledge, the first exploration of the benthic fauna of an ebb-tidal delta with high spatial resolution and extensive abiotic information.

At the ebb-tidal delta, the benthic communities show similarity with sandy communities found for the Belgian part of the North Sea (Breine et al., 2018), the nearshore of the Dutch barrier island Ameland (Holzhauer et al., 2020), and further offshore also the Dogger bank (Kröncke, 2011; Wieking and Kröncke, 2003). The ebb-tidal delta shares its species pool with the surrounding coastline and nearshore and is not characterized by species exclusive to this zone. Nonetheless, very distinctly different assemblages were found. The highest abundance and the highest diversity were found on the plane seaward of the terminal lobe of the delta, as well as on the southern ebb shields. Here, the high abundances mainly originated from high densities of Annelida and Mollusca. In contrast, the more dynamic ebb shields and the deep channels were mainly characterized by Arthropoda. Thus, the benthic communities occupied space according to the geomorphology of the ebb-tidal data.

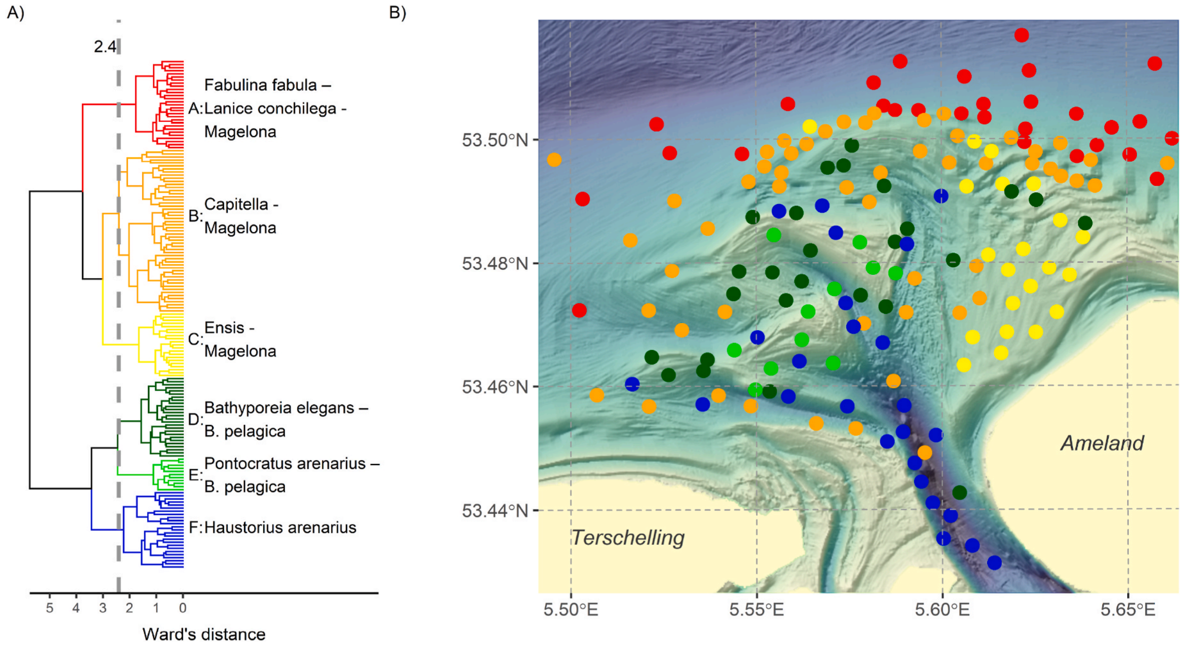


Fig. 5. A) Hierarchical cluster analysis with species abundance, representing six assemblages formed at 2.4 Ward's minimal within cluster variance, B) Spatial distribution of the identified assemblages.

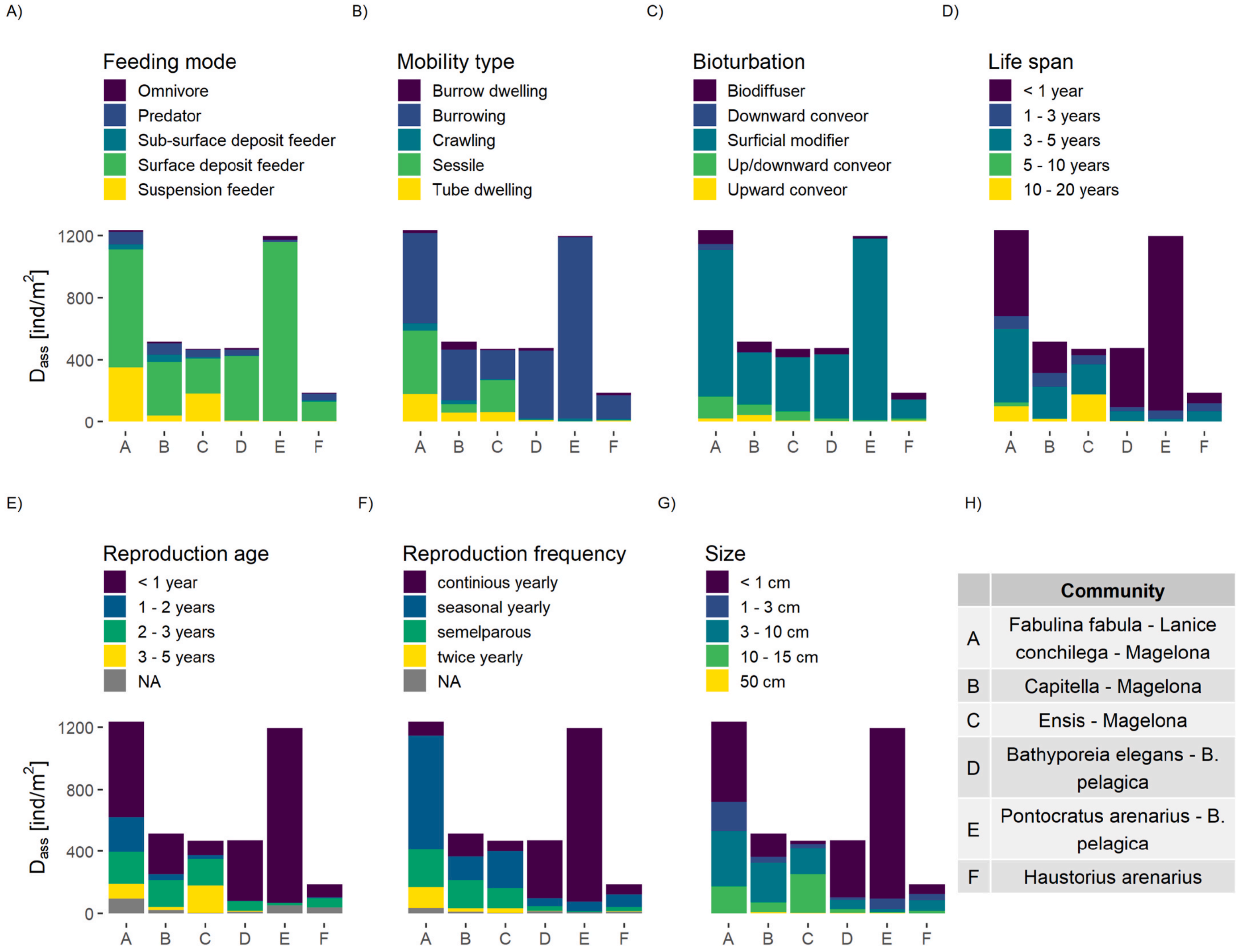
4.1. Benthic communities and their habitat properties

On the basis of abiotic habitat properties, the plane just beyond the terminal lobe of the ebb-tidal delta is characterized as muddy sand habitat, with fine sand, a mud and organic matter content above average, and a less disturbed top layer. The accompanying *F. fabula* – *L. conchilega* – *Magelona* community (assemblage-A) is a diverse community with the highest species density consisting of bivalves and worms. The abiotic conditions are reflected in the functionality of the benthic species. Most of the bivalve species tend to remain in one position in the sediment and the worms construct protective tubes. Such living modes require sufficient sediment stability. For food they filter the overlying water or feed on material deposited on the bed. The *F. fabula* – *L. conchilega* – *Magelona* community shows similarities with the *Bathyporeia-Fabulina* (*Tellina*) community - called "Bank community" – found at the shallow central part of the Dogger Bank (13–20 m water depth). Here the benthic fauna favors the sandy environment with fine sand and a low mud content (<1%) and is capable to withstand the more dynamic conditions at the top of the Dogger Bank (Kröncke, 2011). The main difference is the doubled species number and higher species density of the "Bank community" at the Dogger Bank. Another more coastal region with corresponding sediment grainsizes and benthic communities are the coastal communities *Magelona-E. leei* and *L. balthica* at the Belgian Part of the North Sea (Breine et al., 2018) and the seaward slope of the nearshore bars at Ameland (Holzhauer et al., 2020). Each community has concurring species with the *F. fabula* – *L. conchilega* – *Magelona* community. The average abundance reported for the *Magelona-E. leei* community is twice the abundance of the *F. fabula* – *L. conchilega* – *Magelona* community at the ebb-tidal delta. Where at the seaward slope of the nearshore bars an abundance similar to the *F. fabula* – *L. conchilega* – *Magelona* community is reported. The abundance reported for the *L. balthica* community is halved in respect to the abundance of the *F. fabula* – *L. conchilega* – *Magelona* community and thereby the lowest. The species number of the *F. fabula* – *L. conchilega* – *Magelona* community is the largest followed by the community at the seaward slope of the nearshore bars and the *Magelona-E. leei* and *L. balthica* community at the Belgian Part of the North Sea, respectively. The main difference in the sediment properties of these communities occurs in the mud content, which is much lower for the *F. fabula* – *L. conchilega* – *Magelona* community compared to the *Magelona-E. leei* and *L. balthica* community at the Belgian Part of the North Sea and more in range with the mud content found at the seaward slope of nearshore bars.

The large swash platform, north-east of the Akkepollegat is the habitat of the *Ensis* – *Magelona* community (assemblage-C), a stable sand habitat with a less disturbed sandy bed and some organic matter. This benthic community bears some similarity to the *F. fabula* – *L. conchilega* – *Magelona* community, especially in feeding strategy and mobility. However, this community is less diverse and has a higher proportion of annelids. This is a result of the morphodynamic regime where the main flow is concentrated in the neighboring channels (Akkepollegat, Westgat, and the smaller ebb-chutes) and waves break at the head of the platform resulting in a down-drift sand transport along the ebb-tidal delta margin (Elias et al., 2019). The center of the swash platform is, therefore, more sheltered with a shallow stable seabed (Elias et al., 2020). The dominant species *Ensis* and *Magelona mirabilis*, coincide with the *Magelona-E. leei* community at the Belgian Part of the North Sea. Nevertheless, with an average abundance of only one-fifth of the abundance of the *Magelona-E. leei* community.

The *Capitella* – *Magelona* community (assemblage-B) is found at the margins of the ebb-tidal delta. Compared to the delta-plane, the abiotic conditions here are more dynamic with steeper slopes and coarser sand due to the flow velocity and bed shear stress at the periphery of the ebb-tidal delta and the margins of the channels (Elias et al., 2019). The benthic community at this habitat shows resemblances with both the *F. fabula* – *L. conchilega* – *Magelona* community and the *Ensis* – *Magelona* community. Generally, it is less diverse, with a moderate species number, and an average density compared to the rest of the ebb-tidal delta.

The ebb shields accommodate both the *B. elegans* – *B. pelagica* community (assemblage-D) at the ebb-chutes and the *P. arenarius* – *B. pelagica* community (assemblage-E) at the top of the ebb shields. At the top of the ebb shields the habitat conditions are energetic with breaking waves and sediment being constantly stirred up and transported. This results in medium sand with almost no organic matter. The *P. arenarius* – *B. pelagica* community is a species-poor low-density community where *B. pelagica* occupies a significant fraction of the total density. The species present are well adapted to the energetic conditions with a life span of less than a year. The benthic community coincides with the bar crest of



	Community
A	Fabulina fabula - Lanice conchilega - Magelona
B	Capitella - Magelona
C	Ensis - Magelona
D	Bathyporeia elegans - B. pelagica
E	Pontocratus arenarius - B. pelagica
F	Haustorius arenarius

Fig. 6. Species functional traits within each assemblage. A) preferred feeding mode: **Feeding mode**, B) combination of movement, habit and mobility: **Mobility type,** C) ability of species to alter their environment: **Bioturbation**, D) average life span: **Life span**, E) expected age of reproduction: **Reproduction age,** F) expected frequency of reproduction: **Reproduction frequency**, G) average expected size: **Size**.

the barred coast of Ameland, albeit with a higher species number at the bar crests (Holzhauer et al., 2020). The *B. elegans* – *B. pelagica* community at ebb-chutes is also a species-poor community with a rather low species abundance. The abiotic habitat conditions are dynamic with sediment being pushed seaward over the ebb-chutes towards the ebb-shields where the sediment is deposited (Elias et al., 2019). These conditions are reflected in the dominance of Arthropoda species which are well adapted to dynamic sandy environments. Although species number and abundance are smaller, the community shows resemblances with communities representative for the intertidal beach (Degraer et al., 2003; Janssen et al., 2008) and the shallow slopes of the breaker bars (Holzhauer et al., 2020).

Finally, in the deep channels, a very poor *H. arenarius* community (assemblage-F) was found. The benthic species and functionality are comparable to both the communities of the ebb shields yet poorer with the lowest species density and lowest diversity.

4.2. Dynamic habitats versus less dynamic habitats

In dynamic sandy environments, habitats are under permanent pressure and physical settings can change rapidly, forcing the macrofauna to adapt quickly (McLachlan and Brown, 1990; Snelgrove and Butman, 1994). For the dynamic environment of the Ameland ebb-tidal delta, this is no different. At the dynamic shoals the species were well adjusted to the dynamic circumstances with a short life span, able to burrow through the sand and feed on detritus found on or in the top layer of the sediment. The east side of the ebb-tidal delta is less dynamic and influenced by sediment transported along (bypassing) the ebb-tidal delta (Elias et al., 2019; Lenstra et al., 2019). The species communities here no longer consisted only of surface deposit feeders, but also of suspension feeders. Most species have a longer life span, stay at a fixed location or build tubes and tunnels to live in.

Generally, the number of species, total abundance, and variation in species types were increased in habitats with less environmental stress from waves and currents. In the estuarine conditions of the Western Scheldt, Van der Wal (2017) showed that species richness and total abundance were extremely limited in most of the subtidal channels, but increased significantly where the hydrodynamic stress decreased below critical levels. Similarly in the ebb-tidal delta studied here, very little variation in the benthic community can be seen over the broad range of highly dynamic (either wave-swept or current-swept) habitats. However for the more sheltered and less dynamic habitats, the community composition changes were more clear, as is shown by the appearance of separate communities for the transition zone to the delta-plane, the delta-plane itself, and the wave-sheltered part of the swash platform. The response of the benthic community to gradients in geomorphology

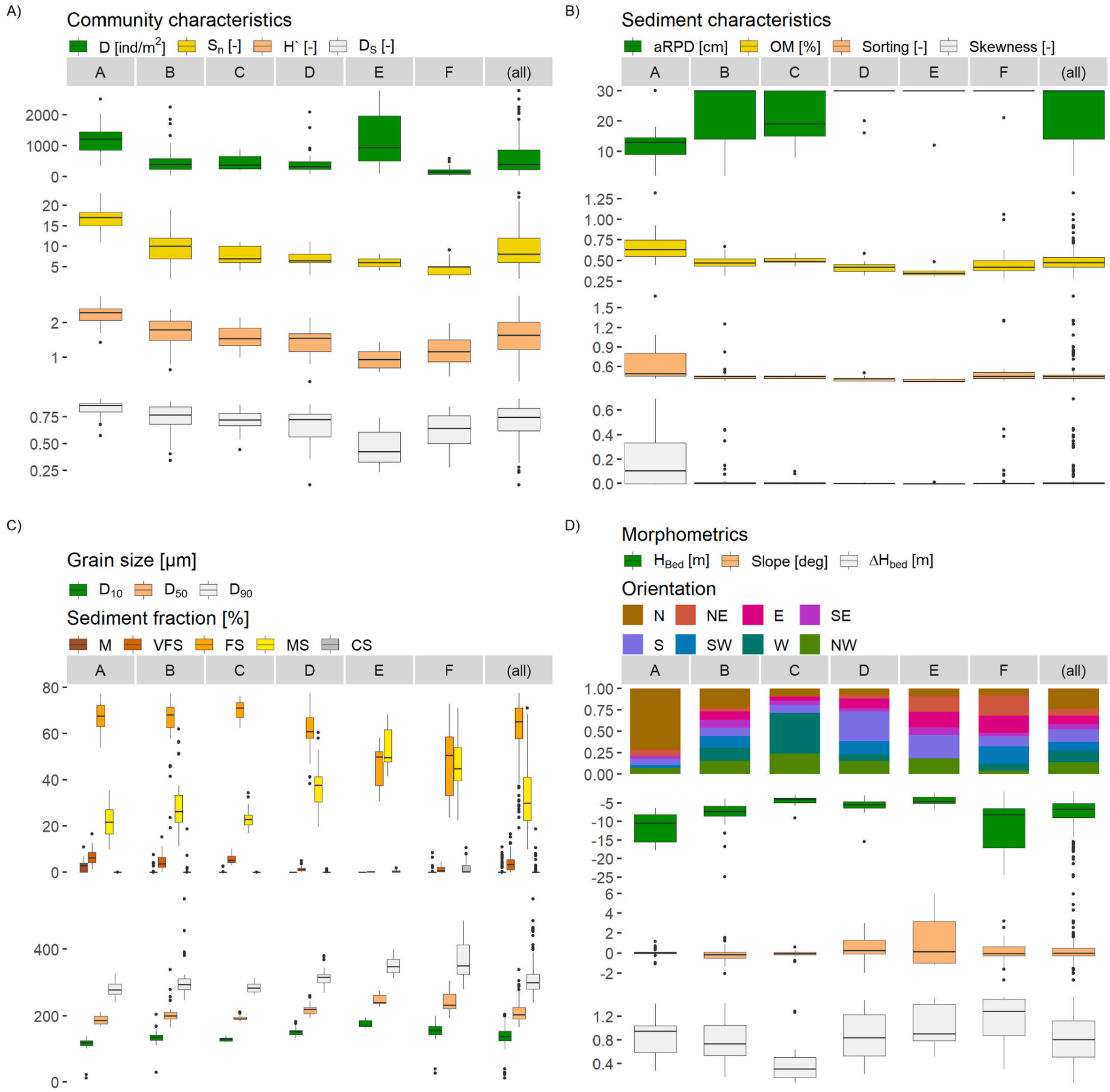


Fig. 7. The species, sediment, and shape characteristics for each assemblage A: Fabulina fabula – Lanice conchilega – Magelona community, B: Capitella – Magelona community, C: Ensis – Magelona community, D: Bathyporeia elegans – B. pelagica community, E: Pontocratus arenarius – B. pelagica community, F: Haustorius arenarius community, and the ebb-tidal delta in general (all).
Panel A) Community characteristics: species density (D), diversity of the assemblage indicated as species number (S_n), Shannon-Wiener-index (H′) and the Simpson-index (D_s). Panel B) Sediment characteristics: the visual depth of the apparent redox potential discontinuity (aRPD), organic matter content (OM) and shape of the grain-size distribution (Sorting and Skewness). Panel C) Sediment grain size of three partitions (10th, 50th and 90th) together with the distribution of sediment fractions (M = Mud, VFS=Very fine sand, FS= Fine sand, MS = Medium sand, CS= Coarse sand). Panel D) Morphometrics represented by bed level (H_{bed}), slope of the bed, bed level change over one year (ΔH_{bed}) and orientation of the bed.

depends on the energetic conditions as we found a decreased species variability over the different environmental conditions in the high-dynamic areas, yet more species variability in the low-dynamic part of the study area.

4.3. The importance of hydrodynamics for refinement of the physiotopes

Based on the complexity of the ebb-tidal delta, we started this research with the identification of physiotopes, areas with homogeneous geomorphology, to give us an optimal spatial coverage and detail as an approach to analyze the benthic species composition and its functionality concerning the environmental information. The physiotopes were not unambiguously found as such in the distribution of the benthic communities. Nonetheless, this study showed that the benthic communities at the ebb-tidal delta were structured along a gradient in the median grain size, organic matter and mud content, and oxygenation of the sediment reflected in the aRPD (Fig. 8). This gradient is, next to the geomorphology, related to the hydrodynamically driven disturbance of the bed due to the general level of physical stress from extremely exposed to waves or currents, to relatively sheltered on the plane just beyond the ebb-tidal delta terminal lobe. Apart from this gradient, a second gradient was found separating between assemblages D and F. Although both environments are stressful and have species-poor and low-abundance assemblages, the species composition is different between the two. From their spatial distribution (Fig. 5) and their average characteristics (Fig. 6), it is clear that this is mainly a distinction between tidal channels (assemblage F) and ebb chutes (assemblage D). The sediment sorting indicates the importance of tidal currents at the main channel (assemblage F) and the delta plane, with moderate to poorly sorted sediment with a very fine skew. Whereas the shoals (assemblage

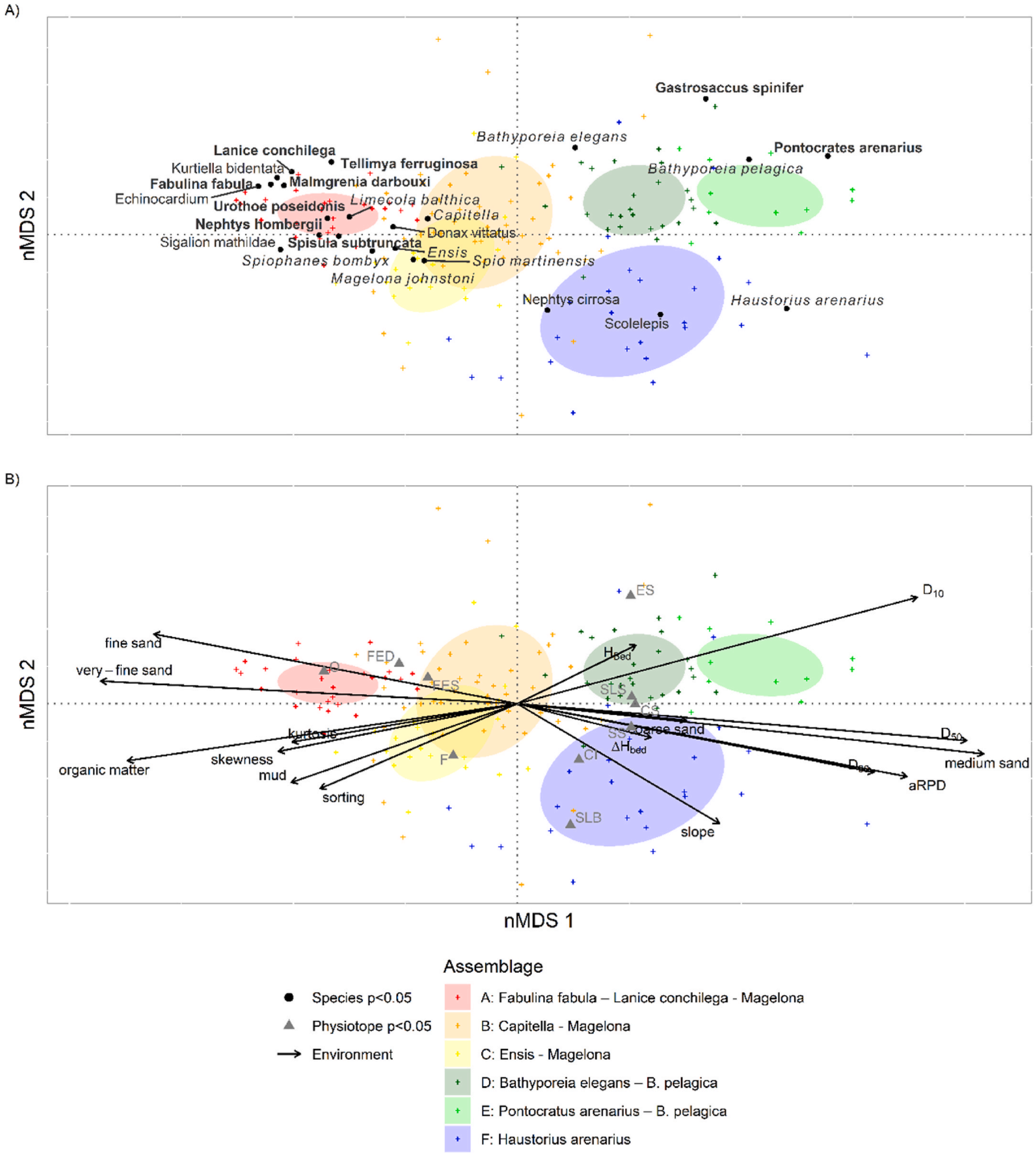


Fig. 8. Nonmetric multidimensional scaling (nMDS with stress = 0.19) ordination of sampling units based on the dissimilarities of fourth-root transformed abundance of the benthic species (44) found at the sampling stations (165) of the Ameland ebb-tidal delta, The Netherlands. The six species assemblages are shown with colored crosses and their standard deviation as an ellipse.
A) Species associated best with the species ordination (ENVFIT $p >$ 0.05). Species in bold are indicator species related to a single assemblage and species indicated in italic are indicator species related to multiple assemblages.
B) The associated environmental parameters, indicated in black. The predefined physiotopes associated with the species ordination (ENVFIT $p <$ 0.05) are indicated in grey (ES = Erosion-Shoal ES, O=Offshore, SLB=Slope-Borndiep, FED=Flank-East-Deep, F=Shallow flat, SLS=Slope-Shoal, CS=Channel-Shoal, SS=Sedimentation-Shoal, FES=Flank-East-Shallow).

D) are more wave impacted with well-sorted sediment and no skewness (Sha and de Boer, 1991). Incorporating detailed hydrodynamic information in the set of environmental parameters could improve the original description of physiotopes. Promising results with the incorporation of near-bed flow processes have been shown in other studies (de Jong et al., 2015; Degraer et al., 2003; van Hoey et al., 2004).

This research encompasses a single ebb-tidal delta. Data from other ebb-tidal deltas as well as a longer time series of the Ameland ebb-tidal delta can enlarge the range of values for the environmental variables and the benthic species. Differences in benthic communities among ebb-tidal deltas may be explained and relationships found with the physiotopes and the environmental parameters can be strengthened and further explored.

4.4. The use of benthic habitat properties for coastal management

Coastal regions are valuable areas with several coastal ecosystem services (Barbier E.B. et al., 2011; Reise, 2002; Snelgrove, 1999; Widdows and Brinsley, 2002). In the Netherlands ebb-tidal deltas are new areas looked upon for nourishments. In 2019 a 5 million m^3 nourishment has been executed at the ebb-shield of the Ameland ebb-tidal delta (Elias et al., 2020). Meanwhile, the ebb-tidal delta of Ameland is part of the coastal ecosystem and protected under the Habitats Directive (European Commission, 1992). This requires reasoning for the selection of locations for activities and indications of potential effects on marine habitats and their communities.

This study shows that the analysis of physiotopes can underpin the functionality of benthic species and thereby the selection of sites for the execution of coastal nourishments. It also shows, however, that the response of benthic communities depends on the extent of the energetic conditions. As long as a broad database documenting the physical-benthic correlation in a large range of conditions is lacking, validation of the significance of the physiotopes for the benthic community will be needed in the execution of large-scale interventions in ebb-tidal deltas.

5. Conclusions

At the ebb-tidal delta of Ameland, a unique dataset of 166 both benthic and sediment samples allowed, for the first time, for an investigation of the benthic macrofauna distribution at an ebb-tidal delta at the spatial scale of its geomorphology.

The assessment of the spatial pattern of benthic communities at the Ameland ebb-tidal delta demonstrated that the benthic species present were typical for the sandy coastal system. The most dominant species were polychaete worms like *Magelona johnstoni,* Arthropoda as *Bathyporeia* and *Urothoe poseidonis* together with bivalves as *Ensis, Limecola balthica* and *Spisula subtruncata.*

The physiotopes were successfully used as a first step to capture the geomorphology of the ebb tidal delta and formed a useful framework for the sampling of sediment and benthic fauna in the field. Including near-bed flow processes and sediment dynamics could improve the description of the physiotopes and the match with the benthic communities present.

The benthic communities found, occupied space according to the combination of geomorphology, sediment composition, mud content, and the accompanying hydrodynamic conditions. Each benthic community differed in species composition and functionality. Mostly sessile species with the largest body size and longevity were found at the muddy sand and stable sand habitat, with the accompanying benthic communities respectively the *F. fabula* – *L. conchilega* – *Magelona* community and the *Ensis* – *Magelona* community. Here sediment composition, mud content, and organic matter were important. At the more dynamic ebb shields, the shape and slope of the bed in combination with wave impact defined the division between the wave-related sands with the *P. arenarius* – *B. pelagica* community and dynamic sands habitats with the *B. elegans* – *B. pelagica* community. Both benthic communities had similar mobility, life span, and feeding strategy. Nevertheless, species abundance was the most distinctive showing a clear division between the communities.

This study found indications of a complex relationship between the extent of the energetic conditions and the benthic community. At the high-dynamic end, species-poor communities are found, that are not very sensitive to a further gradation of the energetic conditions. At the low-dynamic end, communities respond strongly to seemingly small changes in energetic conditions. There appears to be a threshold in dynamic stress below which sessile species and filter-feeders can occur. Where this is the case, species richness is higher and species composition reflects subtle differences in the energetic conditions.

The methodology to derive areas with homogenous environmental conditions can be used to predict the composition of the benthic assemblage, as well as vital traits that are crucial for its capacity to respond to stress (e.g. mobility, reproductive age). The prediction would be enhanced if, apart from information on bathymetry and sediment composition, also hydrodynamic information is included, for example from hydrodynamic models.

Such models have the potential to support predictions of the impact on benthic communities of, for example of the impact of natural changes and human interventions such as nourishment. However, lacking more studies of ebb-tidal deltas and their environment-benthos relations, it is recommended to extensively validate the prediction and expand the available database that can be used as a basis for rational coastal management.

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 Pairwise comparison species and abiotic characteristics

Table A.1
Post hoc pairwise comparison permutation test for each environmental parameter ($p < 0.05$). The significant pairs are shown. Species characteristics: Density (D), species number (S_n), Shannon diversity (H'), Simpson diversity (D_S). Sediment characteristics: organic matter (OM), apparent redox potential discontinuity (aRPD), Sorting, Skewness. Grain-size characteristics: 10th-percentile grain size (D_{10}), median grain size (D_{50}), 90th-percentile grain size (D_{90}). Sediment fractions: fraction mud (M), very fine sand (vfs), fine sand (fs), medium-fine sand (ms), coarse sand (cs). Shape of the bed: bed level (H_{Bed}), slope of the bed (slope), and bed level change over one year (ΔH_{Bed}).

Assemblage Pair	Species characteristics				Sediment characteristics				Grain-size			Sediment fraction					Shape		
A - B	D	S_n	H'	D_S	aRPD	OM	Sorting	Skew	D_{10}	D_{50}	D_{90}	M	Vfs		Ms		H_{Bed}		
A – C	D	S_n	H'	D_S		OM	Sorting	Skew	D_{10}			M					H_{Bed}	Slope	
A – D	D	S_n	H'	D_S	aRPD	OM	Sorting	Skew	D_{10}	D_{50}	D_{90}	M	Vfs	Fs	Ms		H_{Bed}		
A – E		S_n	H'	D_S	aRPD	OM	Sorting	Skew	D_{10}	D_{50}	D_{90}	M	Vfs	Fs	Ms	Cs	H_{Bed}		
A - F	D	S_n	H'	D_S	aRPD	OM		Skew	D_{10}	D_{50}	D_{90}	M	Vfs	Fs	Ms	Cs			
B – C		S_n													Ms		H_{Bed}	Slope	
B – D		S_n	H'	D_S	aRPD	OM			D_{10}	D_{50}			Vfs		Ms		H_{Bed}		ΔH_{Bed}
B – E	D	S_n	H'	D_S		OM			D_{10}	D_{50}	D_{90}		Vfs	Fs	Ms		H_{Bed}	Slope	ΔH_{Bed}
B - F	D	S_n	H'	D_S	aRPD				D_{10}	D_{50}	D_{90}		Vfs	Fs	Ms		H_{Bed}	Slope	
C – D					aRPD	OM	Sorting		D_{10}	D_{50}	D_{90}		Vfs	Fs	Ms		H_{Bed}	Slope	
C – E	D	S_n	H'	D_S	aRPD	OM	Sorting		D_{10}	D_{50}	D_{90}		Vfs	Fs	Ms	Cs		Slope	
C – F	D	S_n	H'	D_S	aRPD				D_{10}	D_{50}	D_{90}		Vfs	Fs	Ms	Cs	H_{Bed}	Slope	
D – E	D		H'	D_S		OM			D_{10}	D_{50}	D_{90}		Vfs	Fs	Ms				
D – F	D	S_n								D_{50}	D_{90}			Fs	Ms	Cs	H_{Bed}		
E – F	D			D_S									Vfs				H_{Bed}		

B Species ebb tidal delta, benthic communities and community characteristics

Table B.1
Species found at the ebb tidal delta and used within the analysis. Species are ranked according to their percentage of species dominance at the ebb tidal delta. The specifications of the benthic species assemblages is given in the columns. For each assemblage, the average species density ($Nm^{-2} \pm sd$) of each species found is given together with the number of locations where this species was found (#loc). Dominant species within the assemblage are indicated in bold. Indicator species are expressed for a single assemblage and combinations of assemblages. Then the predefined physiotopes related to the assemblages are given, with in bold the physiotopes with the best relationship (more than 70% in one assemblage). Assemblages are then characterized by univariate parameters for Species characteristics, Sediment characteristics, Grain size, Sediment fraction, and Shape of the bed.

Community	A	B	C	D	E	F	Ebb-tidal-delta
	F. fabula – L. conchilega - Magelona	Capitella - Magelona	Ensis - Magelona	B. elegans – B. pelagica	P. arenarius – B. pelagica	H. arenarius	
SPECIES							
Bathyporeia pelagica (16.3%)		13 ± 0 (3)	13 ± NA (1)	**221 ± 393 (26)**	**918 ± 814 (11)**	**124 ± 163 (9)**	340 ± 564 (50)
Urothoe poseidonis (12.2%)	**351 ± 364 (29)**	**129 ± 203 (19)**	13 ± 0 (4)	27 ± NA (1)			240 ± 319 (53)
Magelona johnstoni (8.1%)	**99 ± 85 (28)**	**114 ± 153 (39)**	**51 ± 30 (18)**	25 ± 16 (7)		36 ± 20 (3)	88 ± 113 (95)
Bathyporeia elegans (7.8%)	56 ± 54 (11)	**86 ± 97 (43)**	24 ± 16 (6)	**127 ± 141 (25)**	91 ± 105 (5)	27 ± 19 (2)	88 ± 106 (92)
Ensis (6.9%)	**94 ± 87 (28)**	**41 ± 67 (18)**	**177 ± 140 (21)**	16 ± 6 (5)			98 ± 112 (73)
Spio martinensis (6.1%)	**113 ± 84 (28)**	**75 ± 162 (36)**	26 ± 23 (12)	30 ± 25 (4)		15 ± 5 (8)	73 ± 119 (88)
Nephtys cirrosa (5.7%)	30 ± 23 (21)	**50 ± 28 (47)**	**52 ± 44 (19)**	**42 ± 31 (20)**	30 ± 13 (4)	**42 ± 22 (24)**	44 ± 30 (135)
Magelona mirabilis (5.6%)	**63 ± 76 (18)**	**65 ± 57 (34)**	**87 ± 110 (18)**	37 ± 26 (13)	13 ± 0 (3)	**40 ± 43 (10)**	61 ± 70 (96)
Limecola balthica (3.1%)	**84 ± 71 (26)**	31 ± 29 (18)	**53 ± 56 (9)**	13 ± NA (1)		27 ± NA (1)	46 ± 44 (71)
Capitella (3%)	29 ± 19 (20)	**94 ± 260 (25)**	16 ± 5 (6)	13 ± 0 (2)		36 ± 28 (3)	56 ± 176 (56)
Tellimya ferruginosa (2.8%)	**169 ± 131 (15)**	51 ± 84 (7)		13 ± NA (1)		13 ± 0 (2)	81 ± 93 (36)
Pontocrates altamarinus (2.5%)	22 ± 16 (11)	29 ± 19 (40)	21 ± 10 (9)	**30 ± 23 (18)**	29 ± 16 (7)	**30 ± 22 (8)**	28 ± 19 (93)
Spiophanes bombyx (2.4%)	**42 ± 35 (23)**	25 ± 27 (18)	**72 ± 62 (14)**	20 ± 9 (2)		13 ± NA (1)	43 ± 44 (58)
Spisula subtruncata (2.1%)	**107 ± 114 (16)**	75 ± 87 (5)	13 ± 0 (3)			13 ± 0 (2)	83 ± 102 (26)
Pontocrates arenarius (1.5%)		13 ± 0 (2)		30 ± 25 (4)	**122 ± 121 (11)**	27 ± NA (1)	84 ± 105 (18)
Haustorius arenarius (1.4%)				19 ± 15 (7)	65 ± 75 (8)	**53 ± 60 (15)**	48 ± 59 (30)
Lanice conchilega (1.2%)	**40 ± 35 (27)**	13 ± 12 (8)	13 ± 0 (2)				26 ± 22 (47)
Fabulina fabula (1.1%)	**44 ± 34 (24)**	30 ± 25 (4)					32 ± 25 (37)
Scolelepis (1.1%)		26 ± 22 (15)	20 ± 9 (2)	31 ± 21 (12)	16 ± 11 (5)	**25 ± 17 (11)**	26 ± 19 (45)
Nephtys hombergii (1%)	**35 ± 22 (26)**	17 ± 9 (8)				13 ± NA (1)	30 ± 21 (35)
Donax vittatus (0.8%)	31 ± 20 (16)	20 ± 10 (16)	13 ± 0 (2)	13 ± NA (1)			22 ± 15 (38)
Kurtiella bidentata (0.7%)	50 ± 56 (13)	20 ± 8 (4)					37 ± 46 (20)
Nemertea (0.5%)	13 ± NA (1)	23 ± 17 (17)	9 ± 8 (3)	19 ± 12 (5)	40 ± NA (1)		21 ± 15 (27)
Gastrosaccus spinifer (0.5%)	13 ± NA (1)	18 ± 7 (6)		23 ± 13 (4)	30 ± 17 (8)	33 ± 9 (2)	25 ± 14 (21)
Echinocardium (0.5%)	25 ± 17 (14)	27 ± 21 (5)					25 ± 18 (19)
Malmgrenia darbouxi (0.4%)	23 ± 13 (16)	13 ± 0 (4)					21 ± 13 (20)

(*continued on next page*)

Table B.1 (*continued*)

Community	A	B	C	D	E	F	Ebb-tidal-delta
	F. fabula – L. conchilega - Magelona	Capitella - Magelona	Ensis - Magelona	B. elegans – B. pelagica	P. arenarius – B. pelagica	H. arenarius	
Diogenes pugilator (0.4%)	18 ± 10 (8)	21 ± 16 (11)		13 ± NA (1)		13 ± NA (1)	19 ± 13 (21)
Microphthalmus (0.4%)		173 ± 226 (2)				27 ± 0 (2)	100 ± 156 (4)
Nototropis falcatus (0.3%)	22 ± 17 (11)	20 ± 9 (2)	13 ± 0 (2)		13 ± NA (1)	13 ± NA (1)	20 ± 14 (17)
Glycera (0.3%)	17 ± 7 (4)	22 ± 10 (8)		18 ± 8 (3)		13 ± 19 (2)	19 ± 9 (17)
Eteone flava (0.3%)	20 ± 8 (4)	21 ± 22 (9)		13 ± 0 (2)			20 ± 17 (15)
Schistomysis (0.3%)	13 ± 0 (3)	22 ± 10 (8)	17 ± 7 (4)				19 ± 8 (15)
Leucothoe incisa (0.2%)	27 ± 19 (9)		13 ± NA (1)				25 ± 18 (10)
Macomangulus tenuis (0.2%)	17 ± 7 (4)	13 ± 0 (9)	13 ± 0 (2)		13 ± NA (1)		14 ± 3 (16)
Myrianida (0.2%)	33 ± 17 (4)	47 ± 47 (2)					38 ± 26 (6)
Crangon (0.2%)	13 ± 0 (7)	13 ± 0 (3)				18 ± 8 (3)	14 ± 4 (13)
Portumnus latipes (0.2%)	13 ± NA (1)		13 ± NA (1)	13 ± 0 (10)			13 ± 0 (12)
Abra alba (0.1%)	30 ± 25 (4)	13 ± 0 (2)					24 ± 21 (6)
Eteoninae (0.1%)	18 ± 8 (3)	13 ± 0 (5)	13 ± NA (1)				15 ± 4 (9)
Scoloplos armiger (0.1%)	13 ± 0 (2)	13 ± 0 (2)	17 ± 7 (4)			13 ± NA (1)	15 ± 4 (9)
Sigalion mathildae (0.1%)	12 ± 8 (9)	13 ± 0 (2)					12 ± 7 (11)
Cumacea (0.1%)	19 ± 12 (5)	13 ± NA (1)				13 ± NA (1)	17 ± 10 (7)
Microprotopus maculatus (0.1%)	13 ± 0 (2)	40 ± 38 (2)					27 ± 27 (4)
Paraonis fulgens (0.1%)	13 ± NA (1)		13 ± NA (1)	13 ± NA (1)		22 ± 15 (3)	18 ± 11 (6)
PREDEFINED PHYSIOTOPES							
Number of locations	29	53	21	26	11	25	165
Physiotope	EB(2), **FED(6)**, **FES (4)**, FWD(2), **O(10)**, SB(3), SLS(2)	**CB(7)**, CI(2), CS(3), EB(5), **ED(10)**, ES (2), FES(2), **FWD(4)**, **FWS(5)**, O(1), SB(6), F(3), SLB(2), SLS(1)	EB(4), ED(1), **F (16)**	CB(3), CS(5), ES(4), SB(2), SS(5), F(2), SLB(1), SLS(4)	CS(1), ES(4), SS(3), SLS(3)	CB(1), **CI(4)**, CS(2), ES (1), FWS(1), SS(3), F (1), **SLB(7)**, SLS(5)	
SPECIES CHARACTERISTICS							
Density (Nm^{-2})	1236 ± 484	516 ± 453	470 ± 245	475 ± 459	1196 ± 906	188 ± 145	626 ± 570
Species number (-)	17 ± 3	10 ± 4	8 ± 2	7 ± 2	6 ± 1	5 ± 2	9 ± 5
Shannon diversity (-)	2.21 ± 0.3	1.7 ± 0.5	1.57 ± 0.3	1.41 ± 0.4	0.94 ± 0.3	1.18 ± 0.4	1.6 ± 0.5
Simpson diversity (-)	0.83 ± 0.1	0.73 ± 0.1	0.71 ± 0.1	0.66 ± 0.2	0.47 ± 0.2	0.62 ± 0.2	0.7 ± 0.2
SEDIMENT CHARACTERISTICS							
aRPD (cm)	14 ± 8	21 ± 10	21 ± 9	> 30	> 30	> 30	23 ± 9
Organic matter (%)	0.68 ± 0.2	0.49 ± 0.1	0.5 ± 0	0.42 ± 0.1	0.36 ± 0	0.48 ± 0.2	0.5 ± 0.2
Sorting (-)	0.64 ± 0.3	0.48 ± 0.2	0.44 ± 0	0.41 ± 0	0.39 ± 0	0.52 ± 0.2	0.49 ± 0.2
Skewness (-)	0.17 ± 0.2	0.03 ± 0.1	0.01 ± 0	0 ± 0	0 ± 0	0.04 ± 0.1	0.05 ± 0.1
GRAIN SIZE							
D10 (μm)	112 ± 28	132 ± 25	129 ± 6	153 ± 12	175 ± 12	151 ± 40	138 ± 30
D50 (μm)	187 ± 13	205 ± 28	193 ± 8	220 ± 18	248 ± 17	243 ± 32	212 ± 30
D90 (μm)	280 ± 21	306 ± 51	285 ± 14	316 ± 29	350 ± 27	368 ± 61	313 ± 50
SEDIMENT FRACTION							
Mud: <63 μm (%)	2.75 ± 2.8	0.52 ± 1.6	0.26 ± 0.8	0 ± 0	0 ± 0	0.9 ± 2.2	0.81 ± 1.9
Very fine sand: 63 – 125 μm (%)	6.61 ± 3.6	4.49 ± 3.3	5.74 ± 2.1	1.48 ± 1.3	0.14 ± 0.1	1.26 ± 1.5	3.73 ± 3.4
Fine sand: 125 – 250 μm (%)	67.24 ± 5.7	64.66 ± 12	70.02 ± 3.9	60.79 ± 9.8	45.75 ± 9.6	47.74 ± 14.7	61.21 ± 13.1
Medium sand: 250 – 500 μm (%)	21.91 ± 6.7	29.35 ± 11.1	23.74 ± 4.5	37.58 ± 10.4	53.65 ± 9.2	47.27 ± 12.4	33.16 ± 14
Coarse sand 500 – 1000 μm (%)	0 ± 0	0.65 ± 2.8	0 ± 0	0.15 ± 0.4	0.47 ± 0.6	2.28 ± 3.4	0.62 ± 2.2
Shape of the bed							
Bed level (m)	-11.3 ± 3.7	-7.82 ± 3.3	-4.45 ± 1.3	-5.71 ± 2.4	-4.36 ± 1.4	-11.31 ± 6.4	-8.02 ± 4.5
Slope (deg)	0.87 ± 0.3	0.79 ± 0.3	0.41 ± 0.3	0.85 ± 0.4	1.04 ± 0.4	1.11 ± 0.4	0.83 ± 0.4
Bed level change (m)	0.09 ± 0.4	-0.18 ± 0.8	-0.1 ± 0.3	0.51 ± 1.1	1.24 ± 2.6	0.18 ± 1.3	0.13 ± 1.1

C Collinearity abiotic parameters

Table C.1
Collinearity of the abiotic parameters measured. In bold a correlation above 0.8.

	aRPD	OM	D_{10}	D_{50}	D_{90}	skew	sort	kurt	M	VFS	FS	MS	CS	H_{bed}	slope	ΔH_{bed}
aRPD	1															
OM	0.22	1														
D_{10}	−0.19	−0.78	1													
D_{50}	−0.31	−0.43	0.59	1												
D_{90}	−0.27	−0.28	0.4	**0.96**	1											
skew	0.07	0.74	−0.67	−0.09	0.03	1										
sort	0.03	0.7	−0.73	0	0.18	**0.93**	1									
kurt	0.07	0.73	−0.64	−0.09	0.01	**0.97**	**0.89**	1								
M	0.08	0.73	−0.68	−0.05	0.06	**0.97**	**0.9**	**0.9**	1							
VFS	0.27	0.41	−0.55	−0.76	−0.62	0.03	0.07	0.02	−0.01	1						
FS	0.27	0.24	−0.39	**−0.95**	**−0.96**	−0.13	−0.23	−0.1	−0.16	0.62	1					
MS	−0.31	−0.48	0.62	**0.97**	**0.9**	−0.12	−0.04	−0.12	−0.09	−0.78	−0.94	1				
CS	−0.18	0	0.12	0.7	**0.81**	0.15	0.3	0.13	0.17	−0.26	−0.69	0.51	1			
H_{bed}	−0.14	−0.38	0.19	−0.25	−0.36	−0.51	−0.52	−0.47	−0.54	0.11	0.35	−0.17	−0.46	1		
slope	−0.16	−0.01	0.15	0.28	0.24	0.06	0.06	0.07	0.05	−0.26	−0.28	0.29	0.14	−0.26	1	
ΔH_{bed}	−0.21	−0.1	0.12	0.04	−0.02	−0.08	−0.11	−0.08	−0.09	−0.13	−0.03	0.1	−0.16	0.18	0.21	1

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