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Small-scale macrobenthic community structure along asymmetrical sand waves in an underwater seascape

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Abstract

Sand waves are dynamic and regular bedforms that are ubiquitous in sandy shelf seas. However, information about the ecological characteristics (e.g., benthic community structure) and their spatial variability within these habitats is very limited. To address this knowledge gap, we undertook a field campaign in summer 2017 to investigate the macrofaunal community composition of a sand wave area off Texel (Dutch part of the North Sea). Sand waves in this area were asymmetrical, with longer gentle slopes that were approximately double in length to the shorter steep slopes. The benthic distribution along the different parts of these sand waves was assessed by collecting a large number of box cores within a transect line (~1 km). We show considerable variability in the individual, biomass and taxon densities, which were all significantly higher on the steeper slopes of the sand waves. These results are consistent with the trends observed in both the abiotic parameters and video analysis that were measured in two recent studies at the same study area. Our results provide valuable insight into the small-scale patterns of variability in asymmetrical dynamic bedform environments, where gentle slopes seem to be primarily controlled by physical forces, while steep slopes are more under biotic control.

KEYWORDS
biogeomorphology, biological traits and functional traits, macrobenthos, sand waves

1 | INTRODUCTION

In many coastal regions worldwide, the sandy seabed is seldom static or flat, but oftentimes, many types of bedforms can be found, as is the case in the Dutch sector of the North Sea (Borsje, de Vries, et al., 2009). While many of these bedforms are rhythmic in nature, they can be differentiated based on their spatial dimensions. These include the largest sand banks of up to 10 km in length and 30 m in height, down to small sand ripples that are on the order of tens of cms in length and several cms in height; in between this range are several intermediaries such as megaripples (up to 10 m long, tens of cm in height) and sand waves (100–1,000 m long, up to 10 m high; Morelissen et al., 2003). Though development of these bedforms are largely driven by hydrodynamic and physical (e.g., sedimentary) processes, other factors such as benthic organisms are believed to also play an important role in shaping the sedimentary and hydrodynamic conditions of these environments (Borsje et al., 2009; Damveld et al., 2019). This is particularly the case for the meso-scale sand waves, which are the focus of this study here.

Sand waves are found over a range of dimensions and with shapes that can be quite variable, from highly symmetrical to very asymmetrical (e.g., one side is much longer and with a gentler gradient) (Baptist et al., 2006; Barnard et al., 2006; Besio et al., 2008; Liao & Yu, 2005). Similar to other rhythmic bedforms, tidally driven sand waves are commonly found throughout shallow sea environments (e.g., North Sea), as well as some tidal inlets around the world (Besio et al., 2008; Borsje et al., 2014; van Dijk & Kleinhans, 2005; van Santen et al., 2011). In the Dutch sector of the North Sea alone, these sinusoidal features have a wide distribution over a broad range of dimensions (Cheng et al., 2020; Damen et al., 2018). But a key defining feature is their ability to migrate at rates of several meters per year or more (van Dijk et al., 2008; Knaapen, 2005; Németh et al., 2002), making them especially interesting both scientifically and economically. Abundant modeling studies on sand waves have been undertaken over the past decades in terms of the hydrodynamic and morphological processes, using different process-based models to predict their behavior (Besio et al., 2004; Borsje et al., 2013; Borsje, de Vries, et al., 2009; Hulscher, 1996).

In addition to the physical aspects, sand waves are also ecologically important habitats for many benthic invertebrate organisms residing in the seabed, yet there is far less information available regarding the biological and biogeochemical aspects of these environments. All ecosystems invariably undergo natural disturbances, particularly from extreme events such as storms and anomalies in seasonality. However, anthropogenic activities, such as fishing, shipping, sand mining, and oil and gas production, have increasingly been exerting additional pressures on such environments (Halpern et al., 2015; Jennings et al., 2001; Kaiser et al., 2002; de Jong et al., 2016). These activities are expected to further surge in the foreseeable future and are thus of particular relevance for sand wave environments, given their location within regions of high economic interest (Jongbloed et al., 2014). This is further exacerbated by the growing demands for alternative energy sources as well as increasing concerns due to climate change and sea level rise, necessitating ever more coastal protection. As such, many of these areas are anticipated to be impacted by activities such as sand mining or offshore windfarm construction (Vrees, 2019; Deltacommissie, 2008; de Jong et al., 2014, 2016; Jongbloed et al., 2014).

The sediment-inhabiting infauna is well-suited for comparative studies on spatio-temporal benthic ecosystem changes, due to a combination of low mobility and relatively long life spans (Reiss et al., 2010). Furthermore, greater biological diversity in an environment is generally perceived as a positive quality for having higher resiliency to environmental stresses and facilitating higher rates of biological activity such as primary and secondary production, nutrient cycling, and biogeochemistry (Cardinale et al., 2012; Hooper et al., 2005). Moreover, some species within the macrobenthos have been clearly shown to play a significant role in ecosystem functioning by acting as ecosystem engineers (Bouma et al., 2005; Braeckman et al., 2010; Van Colen et al., 2013; Jones et al., 1994). Characterizing these groups based on their functional traits in the context of environment and stressors is a useful way to gain insight about the ecology of a habitat, which is also intrinsically connected to the geomorphology (Dolan et al., 2012; Pearson, 2001). In sand wave environments, organisms that change the roughness of the seabed by the creation of hard structures, by burrowing or excavating the sediment or through their pumping activity (e.g., bioturbation, bioirrigation), may be particularly influential as they alter the sediment distribution. All of these processes, facilitated largely by ecosystem engineers (Jones, 2012; Jones et al., 1997; Meysman et al., 2006), can have consequences for the local geomorphology of the seabed. Moreover, these small-scale processes can even cumulatively cascade up to the sand wave environment as a whole, since ecosystem engineers often exhibit a positive effect on ecosystem functioning by facilitating greater sediment heterogeneity, resource partitioning, biogeochemical activity, and overall habitat stability (Lohrer et al., 2004; Rabaut et al., 2010). Consequently, these conditions can facilitate greater biodiversity by increasing the utilization potential of the given habitat, thereby allowing organisms to make better use of the available resources (space, nutrients, food, etc.; Bruno et al., 2003; Crain & Bertness, 2006), which could then further influence the surrounding habitats (Rabaut et al., 2007).

However, the significance of the benthic community for the ecosystem functioning (e.g., biogeochemical activity, biodiversity, etc.) within the sand wave environment is still largely unclear or inconclusive. Given the logistical challenges of subtidal field sampling, relatively few campaigns have been carried out in these environments, in contrast to the ample studies from laboratory flume experiments or modeling simulations (Best & Kostaschuk, 2002). Thus, field information regarding the sedimentary and hydrodynamic conditions of offshore sand waves are scarce (Janssen et al., 2012; Kleinhans et al., 2009; Paarlberg et al., 2009). Although some of the available field studies have considered more than just the theoretical or physical aspect of sand wave habitats, very few (if any) have specifically focused on characterizing the benthic community composition in the context of their potential influence on the biogeochemical and sedimentological processes along the sand waves, all within the same campaign (Passchier & Kleinhans, 2005; Stolk, 2000; Svenson et al., 2009; Terwindt, 1971; Van Lancker & Jacobs, 2000). Even when available, many of these small-scale studies on benthic communities have been motivated by very specific environmental issues, such as trawling, sand mining or oil and gas work, rather than the direct influence of morphology (Baptist et al., 2006; Kröncke & Bergfeld, 2003). Consequently, much of our understanding about sand waves is derived from modeling studies (Borsje et al., 2014; van Dijk & Kleinhans, 2005; Hulscher, 1996; Van Oyen & Blondeaux, 2009; Van Oyen et al., 2013).

In order to further unravel the spatial variation in both environmental parameters and benthic infauna in a sand wave environment and their effect on ecosystem functioning, a cruise campaign was undertaken on board the NIOZ *RV-Pelagia* in June 2017 to measure not only the environmental parameters, but also determine the sediment characteristics and the benthic community composition in a sand wave area off Texel. Our study complements two other studies from the same cruise. The first was a video transect study of the epibenthic community composition, the endobenthic individual abundance and ripple occurrence/regularity through visual quantification using video footage. The aim of this study was to look for differences between the crest and trough (Damveld et al., 2018). The second study addressed the sediment characteristics along four different areas of the sand waves, and showed a significant difference in the abiotic parameters based on the positioning (Cheng et al., 2020). Based on this information, we hypothesize that geomorphology of the sand wave bedform will have a significant influence on the benthic community structure.

Here, we present new information about the benthic community structure and the associated biogeochemical processes along a sand wave field. We investigate (a) if there is a measurable pattern in how benthic communities are organized along the sand wave continuum, (b) and what the most revealing and extreme functional types of communities may be.

2 | MATERIALS AND METHODS

2.1 | Study area description

All of the benthic macrofauna samples were collected onboard the NIOZ *RV-Pelagia* in the summer (June) of 2017. The study area is a sand wave field situated approximately 22 km to the west of island Texel (53°11.241′N; 4°28.628′E; Figure 1), and these sand waves have a northwest orientation, roughly perpendicular to the coast (Damveld et al., 2018). This area has a relatively sandy seafloor and a water depth between 20 and 30 meters. Prior to sampling, we mapped the study area (~1 km × 3.5 km) with a Kongsberg EM302 Swath Multibeam echo sounder (MBES). The sampling transect and stations were chosen based on the MBES information (Figure 1c). For further technical details about the post-processing of the MBES data and the sampling capabilities and accuracy of the vessel, see Cheng et al., (2020). Adjacent to the sampling area are two shipping lanes that closely flank it on the east and west sides. As a result, the demersal fishing activity is very low in this area (Damveld et al., 2018). The temperature and salinity was approximately 15.2°C and 34.6 ppt. The sand waves ranged from 2.8 to 3.5 m in height and 160 to 210 m in length.

The Texel sand waves are overall sandy in nature with an average median grain size (D_{50}) > 250 μm, and with an asymmetry level of about ~0.29–0.38 (0 is fully symmetrical, 1 is fully asymmetrical). Consequently, the sediment composition, permeability, chlorophyll *a* (chl *a*) and organic carbon largely differed between the two sides, where the gentle slope/crest were on average coarser, with a D_{50} about 40–60 μm higher, compared to the steep slope/trough (Table 1; Cheng et al., 2020). The silt and very fine sand fractions were almost entirely absent on the gentle side of the sand waves. Furthermore, the occurrence of sand ripples also significantly differed between the crest (abundant and regularly shaped ripples) and the trough (low abundance with highly irregularly shaped ripples) (Damveld et al., 2018). As these are important parameters for biogeochemical cycling and the transport of particulate matter and solutes, these spatial patterns could have important ramifications for the benthic community as well.

Sampling was carried out along one transect line, which measured ~1,100 m in length and covered five, full sand waves (Figure 1b,c). We positioned all of our sampling stations along the four highest sand waves to maximize the gradient between the crests and troughs (e.g., the steepness of the sand wave flanks on both sides). In total, 16 stations were positioned at the center of each part of the sand wave (gentle slope, crest, steep slope and trough). The NIOZ Box corer (K6 model) was deployed to obtain macrofauna samples at each station. All samples fell between −32.04 and −28.25 m water depth (Figure 1c).

2.2 | Benthic macrofauna sampling

The dimension of the NIOZ box corer (K6 model) was approximately 32 cm in diameter and 55 cm in length, with the complete frame weighing about 850–900 kg. The entire frame was lowered onto the seabed, followed by the corer being pushed into the sediment by the integrated lead weights. An attached blade sealed the bottom of the box core upon retrieval of the frame. At every station, three replicates were collected with the box corer. In total, 48 samples were collected. All of the sediment collected from each box core was sieved on a 1-mm mesh, preserved in a 4% buffered formalin solution and stored into plastic bottles or buckets, depending on the sample size.

The benthic macrofauna were analyzed by taxonomic experts located on NIOZ-Texel, to the lowest taxonomic unit possible. Each individual was first counted, then weighed. In the latter case, the blotted fresh weight was obtained from each identified sample. This enabled the description of community patterns based on three densities: individual, biomass, and taxon. From this, the main biological traits were also assigned to each taxa based on information from literature (Queiros et al., 2013 and others therein).

2.3 | Habitat identification

2.3.1 | Relative positioning of samples and habitat identification

The position of each box core sample was determined relative to its respective sand wave, because each of them were slightly different in length and height (Figure 1c); this way, it would be possible to compare all samples. Based on the average asymmetry of the sand waves, each one was then rescaled to a range of −1.0 to 0.53, with both ends representing the troughs and the crest situated at 0.0. The unequal scale approximates the asymmetry of the sand waves, where the gentle side is roughly double in length to that of the steep side. The macrofauna individual counts, biomasses, and taxon densities were first compared on this relative scale to show the total distribution.

In addition, the box corer samples were initially categorized using a similar methodology from Cheng et al., (2020), where the sand waves were divided into four morphological units (MUs): gentle slope, crest, steep slope, and trough. This was determined based on

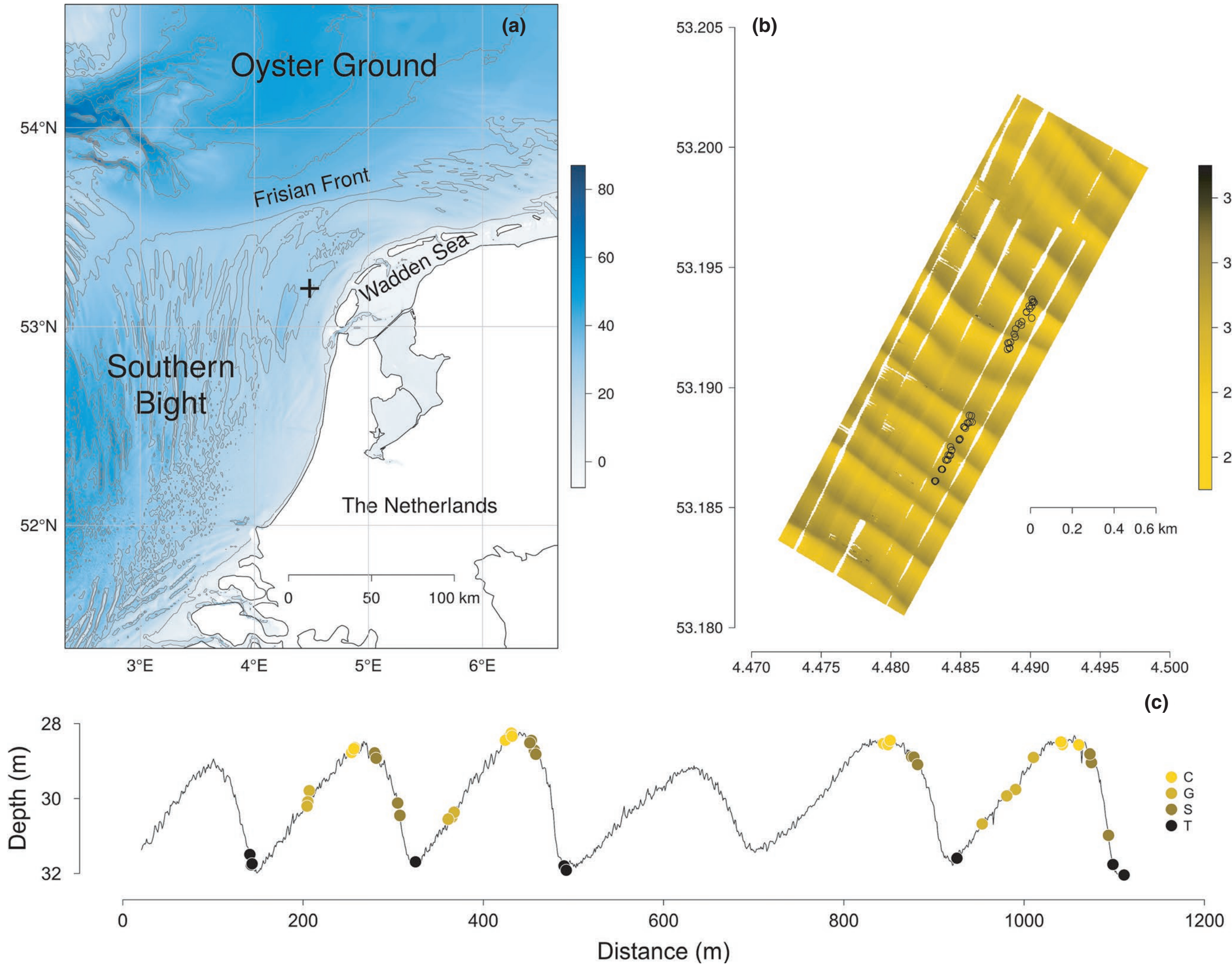

FIGURE 1 Study area. (a) "+" indicates the location of the studied sand wave field in the southern North Sea. (b) Close up of the sand wave field (processed and gridded MBES data); dots indicate benthic sampling stations. (c) Cross section of the sampled transect from south to north; dots, benthic sample locations ($n = 48$): "G," "C," "S," and "T" for gentle slope, crest, steep slope, and trough habitat, respectively. Color bars in a and b indicate depth in meters

TABLE 1 Select sediment parameters between the different habitats (data from Cheng et al., 2020)

	Crest		Gentle slope		Trough		Steep slope	
Variable	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*
Permeability (m^2)	2.54 E^{-11}	$\pm 5.17 \text{ E}^{-12}$	2.45 E^{-11}	$\pm 3.13 \text{ E}^{-12}$	1.64 E^{-11}	$\pm 7.3 \text{ E}^{-12}$	0.901 E^{-11}	$\pm 3.99 \text{ E}^{-12}$
D_{50} (µm)	322.9	±16.27	326.5	±3.69	279.4	±41.1	262.9	±5.998
Org. carbon (%)	0.023	±0.008	0.026	±0.008	0.097	±0.185	0.071	±0.035
chl *a* (µg g^{-1})	0.69	±0.47	0.25	±0.05	1.02	±0.48	1.94	±1.76
Water depth (m)	−28.53	±0.14	−30.08	±0.52	−31.75	±0.16	−29.27	±0.85

Abbreviation: *SD*: standard deviation.

the original dimensions of each respective sand wave, and not the rescaled one. As with the previous study on the sediment characteristics, this method also yielded satisfactory results for the community composition categorization, overall. However, initial statistical analyses showed a strong dichotomy between the stations located within the gentle slope-half of the crest versus the stations found very near the interface between the crest and steep slope. Thus, the latter stations were grouped with the other steep slope stations instead, but no further modification was made to the methodology. For the purposes of the macrofauna distribution, each of these MUs was considered as a separate "habitat" within the sand wave, and all references will use this terminology thereafter.

2.3.2 | Benthic community analyses

Firstly, we investigated the organism density trends along the sand wave gradient; the significance of habitat effect was assessed by Kruskal–Wallis rank sum test (Kruskal & Wallis, 1952) and Dunn test (Dunn, 1964). The latter is a non-parametric post hoc test that is used to show where the significant differences are occurring. Since the analyses involved multiple comparisons on the same variables, a Bonferroni correction was also applied. This limits the chance for Type 1 errors by lowering the alpha value. Then, we explored the community structure across the four habitats by means of a Between-Class Analysis (BCA; Dolédec & Chessel, 1987; Thioulouse et al., 2018). BCA builds axes of maximum covariances between the taxa that discriminate each habitat to the greatest extent. Prior to the BCA, we processed *ln*-transformed individual densities of organisms by centerd Principal Component Analysis (PCA). The effect of the habitat on the variation of community structure was tested based on 999 random permutations of the samples × taxa matrix (Manly, 1991). BCA is equivalent to a Redundancy analysis (RDA) when performed on a unique qualitative explanatory variable (i.e., habitat partitioning, as in the case of our study). Hence, in this specific context, the use of BCA enables us to specifically emphasize on the variations in community composition solely due to habitat specificities, unlike through basic PCA or nonmetric multidimensional scaling (nMDS), both of which could encompass additional sources of variations (e.g., variations in abundances of generalist species).

We completed the investigation on community structure by using biological traits that could account for taxon distributions among the different habitats. Body mass was considered to reflect habitat production and, together alongside motility, burrowing depth and feeding type, as adaptations to sediment properties (Pearson, 1978). We also considered sediment mixing types to account for potential biogeochemical properties of habitats (Queiros et al., 2013). The biological trait data were combined with field data by aggregating within-trait organism densities per sample to generate a samples ×trait modalities matrix (community weighted mean; Kleyer et al., 2012). Analyses and graphical representations were done with R 3.6.3 (R Core Team, 2019); BCA with the package "ade4" (Chessel et al., 2004).

3 | RESULTS

3.1 | Community patterns

3.1.1 | Trends in organism densities

In total, 63 different taxa were identified in the samples. The taxa which could not be identified to species level and, concurrently, had a similar function to other closely related taxa were combined at the same taxonomic group (e.g., *Genus* sp.). By rescaling each sand wave, we compared all of the samples based on their relative positions (Figure 2a–c). High density values were mostly concentrated on the steep slope (relative distance > 0) and, to a lesser extent, in the trough, at least for taxonomic and individual densities. A clear habitat effect was detected (Kruskal–Wallis test, p <.001), with steep slope densities being systematically the highest, and trough densities being intermediate (Figure 2e,f). Steep slope taxon and individual densities were ca two times higher than in the other habitats, and ten times higher for biomass.

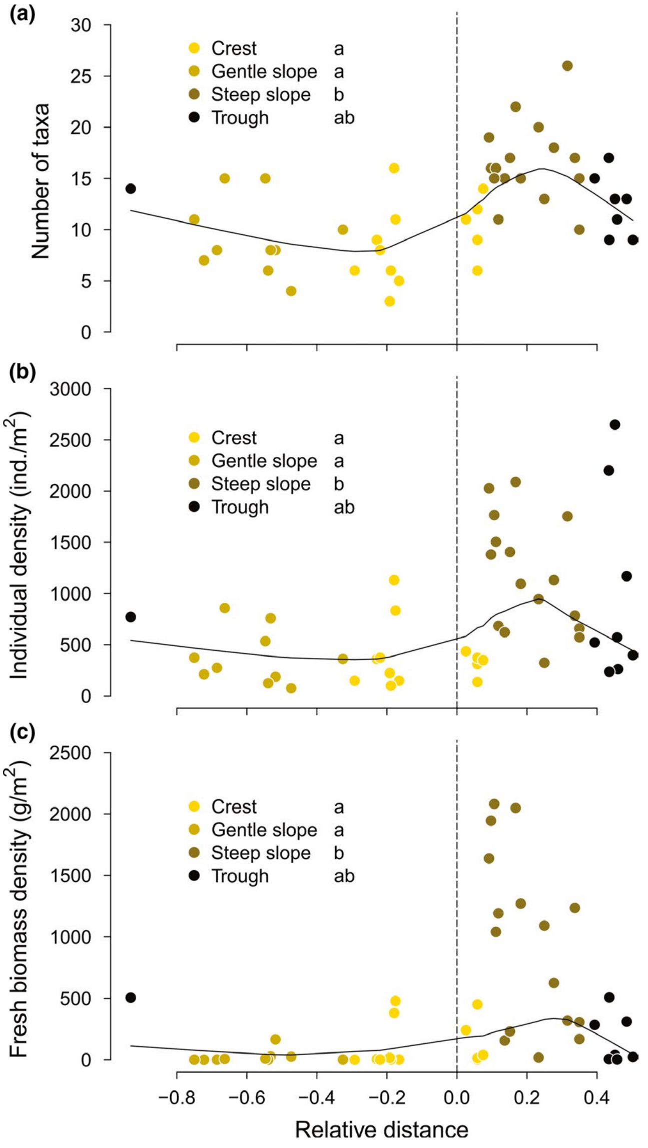

FIGURE 2 (a–c) Relative positions of organism densities along the sand wave continuum; black line, non-parametric Lowess fitting; color dots, organism densitiesper habitat (e.g., MU); common letters indicate no statistical difference according to multiple comparisons of Dunn test with Bonferroni correction

3.1.2 | Taxonomic composition

A prominent feature of faunal distributions among the four habitats was the taxonomic specificity of the steep slope that hosted 53 taxa, of which 13 were specific only to this habitat (Figure 3). Although *Corophium* sp. and *Syllis gracilis* were specific to trough,

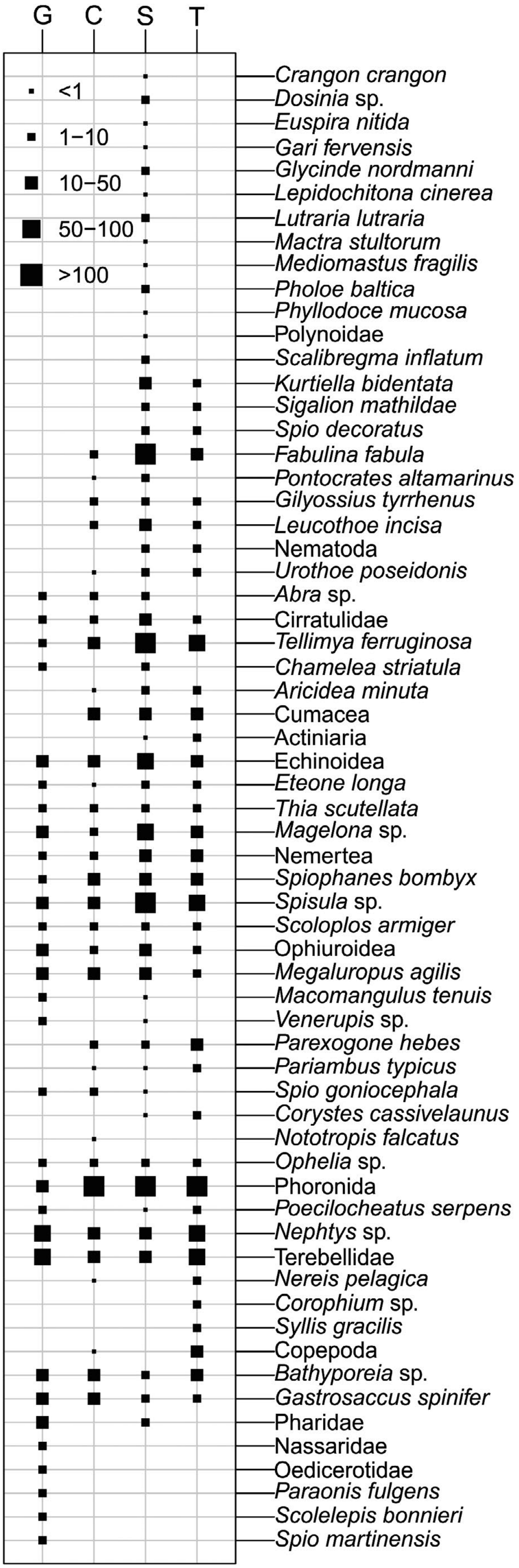

FIGURE 3 Taxon distributions along the sand wave continuum; "G," "C," "S," and "T" for gentle slope, crest, steep slope, and trough habitat, respectively. Taxa are sorted according to niche preference (horizontal profiles). Square size expresses average individual density (ind. m^{-2})

and Nassaridae, Oedicerotidae, *Scolelepis bonnieri*, and *Spio martinensis* to gentle slope, these taxa were low in abundance, such that most of the communities from the gentle slope, crest, and trough were actually also subsets of the steep slope community. Among the more abundant taxa, Echinoidea, *Magelona* sp., *Nephtys* sp., *Spisula* sp., and Terebellidae were the most common to the four habitats. Crustaceans such as *Bathyporeia* sp., *Gastrosaccus spinifer*, and *Megaluropus agilis* were very characteristic of the gentle slope, along with Pharidae and Ophiuroidea. Phoronida, although present in all four habitats, was the least abundant on the gentle slope, where seven other taxa had a higher abundance. In contrast, Phoronids were the most dominant on the crest, but also co-occurring with the dominant taxa of the gentle slope (*Nephtys* sp. and Terebellidae). On the steep slope, Phoronids were third most abundant (second among the habitats in absolute terms) next to the dominant *Tellimya ferruginosa* and *Fabulina fabula*, followed by *Spisula* sp., Echinoidea, and *Magelona* sp. In the trough habitat, Phoronids were the most dominant of all, co-occurring with the dominant taxa of *Spisula* sp. and *T. ferruginosa* from the steep slope. However, there was a substantial drop of *F. fabula* density and the trough was instead more characterized by *Parexogone hebes* and Copepoda.

Although biomass exhibited the same trend as individual density along the sand wave continuum, it was much less evenly distributed among taxa. Indeed, more than 90% of the total biomass was comprised by Echinoidea (mainly represented by *Echinocardium cordatum*), of which 80% was concentrated on the steep slope. Another highly dominant taxon, *F. fabula*, also largely contributed to the total biomass of the steep slope, followed by *Gilyossius tyrrhena*, which was only absent from the gentle slope. Detailed densities of the ten most abundant and heavy taxa of each habitat are listed in the supplementary material (Table S1).

3.1.3 | Community structure

BCA revealed a significant habitat structuring in terms of community composition (Figure 4). Habitat explained 24% of the variation ($p < .001$), mostly along the first axis. This gradient contrasted the highest densities encountered in the steep slope to densities from the other three habitats (Figure 4b). Furthermore, the BCA showed that all four habitats could be clearly distinguished by combining compositional aspects. Surprisingly, community ordination was not dominantly expressed following the geomorphological continuum, for example, from trough to the gentle slope, crest, steep slope, and again back to trough. Along the first axis (horizontal), from left to right, the trough immediately progressed to crest, and not the steep slope, the latter being positioned according to a density gradient (Figure 2). In addition, within-habitat variation increased along this gradient, with the gentle slope encompassing the most homogeneous community. From gentle to steep slope, the trend was driven by the most abundant or density-specific taxa such as *T. ferruginosa*, *F. fabula*, Echinoidea, *Spisula* sp., and *Magelona* sp. (Figure 4a). Whereas this gradient was due to a size effect overall, in which most of the taxa covaried positively together (e.g., the same direction in the ordination plot), there were specific crustaceans (*Bathyporea* sp. and *G. spinifer*) on the gentle slope which deviated from this trend. The second axis (vertical) was predominantly expressed by Phoronida, which was highly characteristic of the trough. However, the variability of the second axis was also explained by ubiquitous taxa that represented a substantial part of the densities of the crest (Phoronida, *Spisula* sp. and *T. ferruginosa*), trough (Phoronida), and steep slope (*F. fabula* and *T. ferruginosa*); the trough and steep slope habitats were inflated in part by the dominant taxa reaching maximum densities in these two habitats. The third axis (Figure 4c,d, vertical), although expressing only a slight part of the total variation in community structure, interestingly exhibited the spatial contiguity between the gentle slope and trough (Terebellidae, Nemertea, *Nephtys* sp. and *Bathyporeia* sp.) in the lower part of the factorial plane to the contiguity of the steep slope and crest in the top (*Spio gonocephala*, *Leucothoe incisa*, *Spisula* sp., *and F. fabula*). This plane reconstituted the spatial habitat succession in a circular way (Figure 4d), from trough (bottom right) to gentle slope (bottom left), then transitioning to crest (top left) and completing the cycle in the steep slope (top right). The top 10 highest and lowest ordination scores from each axes are shown in the supplementary material (Table S2).

3.1.4 | Biological traits

In total, 63 taxa were documented for traits, encompassing 96% of the total individual organism count. The trait modality distributions along the sand wave continuum are shown in Figure 5. In each of the traits distinguished, some modalities were clearly dominant in the benthic communities in certain habitats along the sand wave (Figure 5). Overall, the organisms were on average of small body mass, predominantly crawlers, followed by tubicolous, and mostly surficial modifiers, followed by sediment diffusors. From the gentle slope down to the trough, monotonous trends were detected for small body mass, which increased at the expense of the intermediate body mass (Figure 5a). In addition, the burrowing depth progressively switched from surface dwellers to deeper burrowers toward the trough from both flanks (Figure 5c). To a lesser extent, the swimming ability also decreased along the gradient, being the highest on the gentle slope, followed by the crest and then the lowest on both the steep slope and trough (Figure 5b). Also, somewhat more specific on the steep slope was that the motility was predominantly represented by crawlers while exhibiting a substantial drop in tubicolous worms. In most cases, when a significant effect was detected within a given trait modality, it was induced by the extremes in the percentages of taxa that was found between the gentle and steep slopes, with negligible difference between the steep slope and trough. This was also the case for the opposing trends observed between the suspension feeders, which were highest on the steep slope, and carnivorous–scavengers, which were the lowest there (Figure 5d). Percentages of both surficial modifiers and deep burrowers were the highest on the steep slope especially since some from the latter group (e.g., phoronids, *Urothoe poseidonis*, and a few bivalves) can affect the sediment surface. In summary, the gentle and steep slope habitats appeared to consistently exhibit the most extreme functional types through their contrasting taxonomic oppositions (Figure 4).

4 | DISCUSSION

The sand waves in Dutch waters exhibit a shift of increasing asymmetry toward the coastal regions (Cheng et al., 2020). As recent studies have shown, such morphological differences (e.g., asymmetry) have resulted in significant, small-scale variability in the sediment characteristics (Table 1), bed roughness as well as benthic organism densities (Cheng et al., 2020; Damen et al., 2018; Damveld et al., 2018). In this study, we showed that the morphology of the asymmetrical sand waves have a profound effect on the benthic community structure, as seen in the individual, biomass and taxon densities. Yet, the closer proximity to the coast also increases the likelihood for these asymmetrical sand waves to be impacted by human activity, either directly through fishing activity, such as bottom trawling, dredging or installation of hard infrastructure, or indirectly from the resulting changes in hydrodynamics and/or sediment properties (Bergman & Hup, 1992; Coates et al., 2013; Eigaard et al., 2016; Maar et al., 2009; Reubens et al., 2014; Tillin et al., 2006; van Denderen et al., 2014). Thus, it is necessary to gain a thorough understanding of the different, but linked, processes in these sand waves in order to be able to predict the magnitude and type of impacts that could result. There is presently a knowledge gap regarding the interrelations in the biogeomorphology over a small spatial scale within a dynamic bedform environment, which was the main motivation for our study.

Conducted a long time ago, the North Sea Benthos Survey (NSBS) still provides a large scale reference work on macrobenthic communities (Heip et al., 1992). At the large scale, the particular benthic assemblages correspond well to factors including sediment chl *a* content, silt content, grain size, percentage of organic carbon, location (latitude), and water depth. Largely from the latter two factors, three distinct regions have been identified (northern, central and southern) (Heip et al., 1992). Künitzer et al., (1992) further subdivided the North Sea into eight regions based on depth contours, followed by sediment type. Even more assemblages were found when analyzed at a finer scale, as was done in the study by Duineveld et al., (1990), which looked specifically at the Dutch sector of the North Sea. While they categorized the region into four subareas based on topography, bathymetry, and grain size, there were in actuality, two distinct regions of benthic assemblages between the north and south, the latter of which encompasses the Texel sand waves. To a certain extent, the classification of entire areas or regions into benthic assemblages is a matter of scale (Künitzer et al., 1992). The aforementioned studies all made use of data from the same campaign, but came to different conclusions largely due to a change in the scale of analyses. Our results suggest that sampling resolution is another important aspect that must also be considered, especially for dynamic environments such as asymmetrical sand waves.

The difference in spatial scale (NSBS stations were each >40 km apart with 5 box cores and/or van Veen grabs; our stations were tens of m apart with 3 box cores each) between Duineveld et al., (1990) and our study still presents limitations for extrapolating habitat-specific conditions or associated trends in benthic assemblages. For instance, we found some commonalities in dominant taxa between the southern Dutch North Sea habitat and our study site (e.g., *E. cordatum*, *Magelona sp.*, *Bathyporeia sp.*, *T. ferruginosa*, and *F. fabula*), but the NSBS data does not contain high enough resolution to show how, where or why our taxa are spatially distributed across the sand waves. While the abiotic parameters (e.g., grain size, water depth, etc.) are largely consistent, the species richness of all four of our habitats are at or above the upper range of those measured from the southern region. The steep slope with 53 taxa is actually within the average of the northern region. As a result, our data demonstrates that a large-scale campaign, with lower sampling resolution, could very well result in an underestimation of the actual taxon richness, even in the taxonomically poorer Southern Bight. Furthermore, the variation in richness is also much greater (30–53 taxa in our samples versus. ~20–30 in the southern region, based on the NSBS). Again, the range observed between our four habitats overlaps more with the northern region near the muddy and more species rich Oyster Ground (~40–70 taxa). This is especially interesting, given that sandy environments as the Texel sand waves are typically believed to be less biologically diverse compared to the more muddier environments (Duineveld et al., 1990; Heip et al., 1992; Künitzer et al., 1992; Santos et al., 2012). Our results suggest that local variability could well exceed what has been observed from regional trends, including in regions that are more species rich. Over a small spatial scale of only tens of meters or less, we were able to measure significant differences in the benthic community structure at much higher levels than what has been found for the southern region of the Dutch North Sea in previous studies. Such observations could bring new insight into the biogeomorphological dynamics of rhythmic bedforms in shallow coastal seas, specifically in the benthic community structuring.

4.1 | Geomorphological effects on community structure and associated biological traits

A minute difference in strength between the tidal residual flow (~0.05 m/s) is sufficient to provoke sand wave migration of up to several meters or more per year (Borsje et al., 2013), as well as develop sand wave asymmetry. Although the later process is estimated to occur on time scales of multiple decades based on modeling studies (Damveld et al., 2019; van Gerwen et al., 2018), it is not certain how and whether this would affect the biological communities. While the predominant flow is slightly stronger in the flood than ebb direction, which drives the migration of sand uphill on the gentle slope to the crest, it seems unlikely that there would be much sheltering during ebb flow. Interestingly, there is a near-absence of sessile taxa in all samples, which likely reflects the relatively mobile nature of sand waves, which are less favorable to immobile groups (Pearson, 2001). This appears to be the case even in the troughs, which are largely devoid of fast-moving bedforms such as sand ripples (Damveld et al., 2018). However, the exact flow dynamics are not readily available along these sand waves, and care must be taken in interpreting these patterns. What is clear is that both the abiotic measurements along the sand wave (Cheng et al., 2020) and the ripple and epibenthic density differences between the crest and trough (Damveld et al., 2018) suggest flow conditions to be significantly different between each habitat.

Different hydrodynamic conditions along the sand wave environment may be a major explanation of benthic community structuring. Generally speaking, tidal velocities lower than 16 cm/s enable organic matter to settle (Creutzberg et al., 1984), such that the combined variations in physical and sediment properties can result in an alternative benthic community structure. What is generally observed on a larger scale, and according to the stability-time hypothesis (Sanders, 1968), is that a higher physical stability enables more individual organisms to survive, thereby supporting a higher number of species overall. Benthos that inhabit the upper layers of sediment are adapted to the flow rates near the bed (Pearson, 2001) and although not the only factor, hydrodynamics can select stress-resistant organisms or affect sediment deposition rate. The highly unequal distribution of macrofauna densities along the studied sand waves seems to suggest that similar ecological patterns may also be established and distinguishable at the smaller-scale. Community diversity tends to increase in environments that are more heterogeneous in sediment composition and more stable over time (Pearson & Rosenberg, 1977; Sanders, 1968), as appears to be the case for the steep slope and troughs. The individual abundance, biomass, and taxon density all showed a pattern of distribution consistent to the abiotic variables between each of the habitats (Cheng et al., 2020).

Likewise, the physical movement of sediment can have important consequences, especially for certain feeding groups such as deposit feeders or suspension feeders. On the one hand, tube-building worms (tubicolous) and burrowing animals can increase the sediment surface area significantly enough to enhance the exchange rates with the overlying water (Forster et al., 1999; Santos et al., 2012; Stieglitz et al., 2000). However, increased deposition (e.g., elevated levels of silt and organic matter) could exclude less mobile species with a limited ability to escape burial or clogging of their feeding apparatus (Lohrer et al., 2004; Mestdagh et al., 2018). This is significant as some benthic organisms can redistribute the upper layers of sediment and enable the burial of fine material, particularly as their densities become higher (e.g., steep slope and trough) (Santos

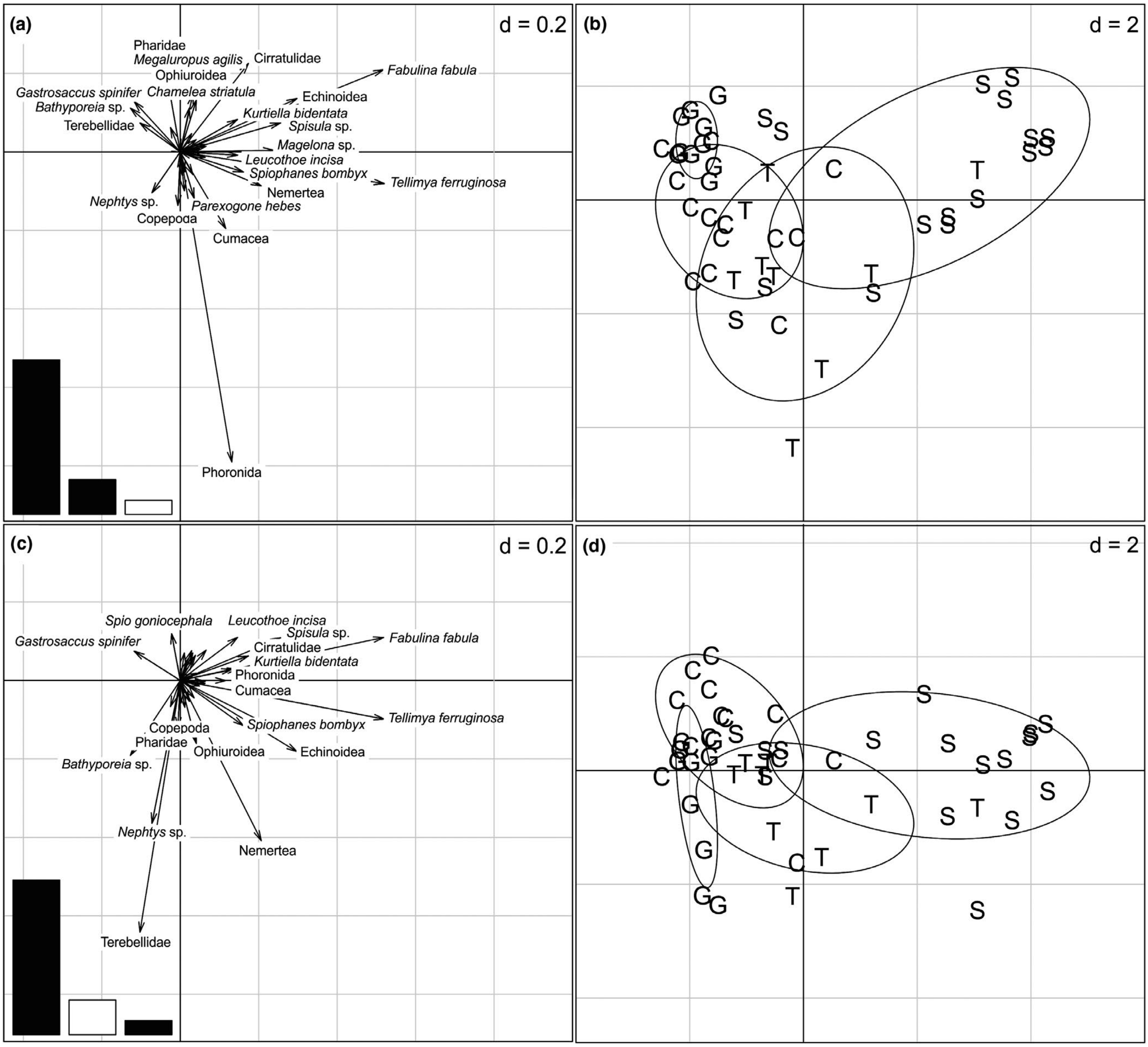

FIGURE 4 BCA; top, axes 1 and 2; bottom, axes 1 and 3. (a and c) Projections of the taxa; for clarity, only taxa with substantial contributions are labelled; bar diagram, eigenvalues. (b and d) Samples grouped per habitat; "Gentle slope = G," "Crest = C," "Steep slope = S," and "Trough = T." "d" indicates the grid scale

et al., 2012; Volkenborn et al., 2007). Evidently, the steep slope contained high numbers of deposit feeders while the tube-building worms were much less frequent compared to the trough. But overall, our data demonstrated that the majority of the taxa prefer the finer, siltier steep slope, and trough habitats. Concurrently, these areas consistently exhibited higher chl *a* and organic matter concentrations (Table 1), indicating a higher availability of food resources (Bauer et al., 2013; Cheng et al., 2020; van Nugteren et al., 2009). Our results are consistent to previous studies that have found higher diversity in both small and large rhythmic bedform troughs, which also tended to be finer in sediment composition (van Dijk et al., 2012; Damveld et al., 2018; Mestdagh et al., 2020; Ramey-Balci et al., 2009; Tilman, 1982; Van Lancker et al., 2012). In contrast, the gentle side of the sand waves, which was coarser, more permeable and lower in organic material (Cheng et al., 2020), had by far the lowest diversity and biomass, despite encompassing a larger surface area than the steep slope. The taxa on the gentle slope clearly exhibited the most homogeneity in community structure, and the few taxa which stood out in this habitat included the mobile fauna such as the swimmers (e.g., *Nephtys* sp., *Bathyporeia* sp., Ophiuroidea, *G. spinifer*, and Terebellidae).

Moreover, the asymmetrical nature of these bedforms can also give rise to different levels of bed roughness, as was shown in the video transect study at the Texel sand wave area by Damveld et al., (2018). Such variability in size and the type of bed feature, particularly smaller ones, is known to be relevant for the biology

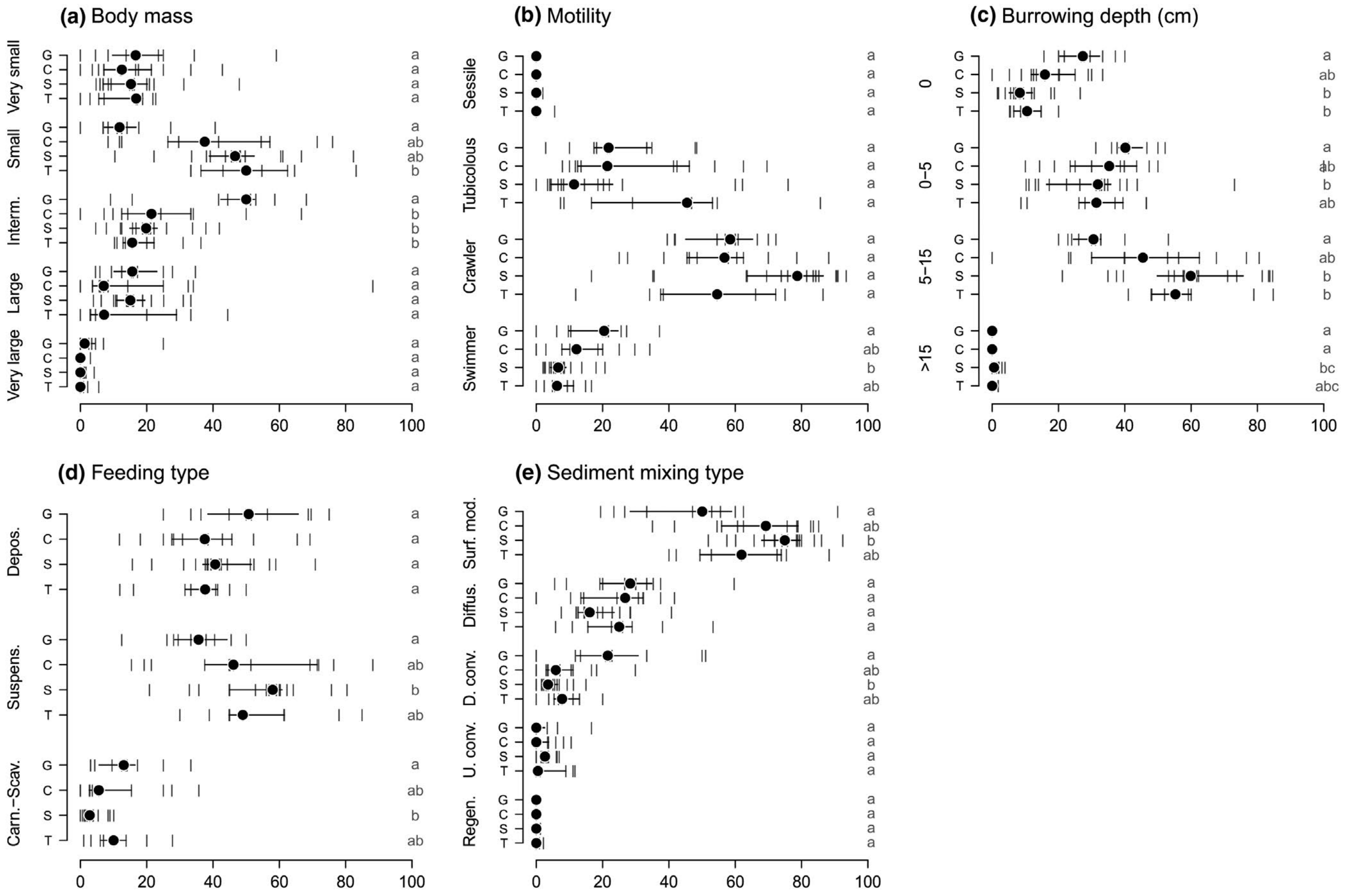

FIGURE 5 Within-trait distributions of individual densities of the taxa. For each trait modality, densities are distributed along the sand wave continuum (habitats): "Gentle slope = G," "Crest = C," "Steep slope = S," and "Trough = T." (a) Body mass. "Interm.," intermediate. (b) Motility. (c) Burrowing depth (cm). (d) Feeding type. "Depos.," deposit feeding; "Suspens.," suspension feeding; "Carn.-Scav.," carnivory-scavenging. (e) Sediment mixing type. "surf. mod.," surficial modifier; "Diffus.," diffusers; "D. conv.," downward conveyor; "U. conv.," upward conveyor; "Regen.," regenerator. Values are expressed in percentages of total individual density for each trait within each of the four habitats; gray vertical segments are sample observations; black dots represent median values; bars extend from 25th to 75th percentiles. Common letters indicate no statistical difference according to multiple comparisons of Dunn test within trait modality with Bonferroni correction

(Dolan et al., 2012). The troughs contained very few, irregularly shaped sand ripples as opposed to the high regularity and number of ripples at the crests. Concomitantly, these authors measured four times the number of epibenthos and observed 30 times more holes (a proxy for endobenthos) in the troughs. The differences we found between the crest and trough, although somewhat lower (only up to 2.9 times higher abundance in the trough), is consistent with these observations. But more importantly, we found larger extremes in diversity and biomass between the two types of slopes; unfortunately information about the roughness in these habitats is not available as the video study only focused on the crest and trough. The variable bed roughness could have important consequences in these permeable sands, where ripples exert pressure differences induced on the sediment surface which allows flows to penetrate through the sand grains (Huettel & Gust, 1992; Jenness & Duineveld, 1985; Rusch & Huettel, 2000). This process, which entrains solutes and fine particles that accumulate under low to moderate flows while being carried out of the sediment at higher flow conditions, may partially explain the elevated levels of fine particles on the steep slope and trough (Cheng et al., 2020). As the physical steering via currents diminishes, the influence of bioturbation becomes increasingly important (Pearson, 2001), especially when coupled with the simultaneous decrease in permeability. Thus, the drastic decrease in ripples in the troughs, coupled with the simultaneous decrease in permeability, restricts physical transport in and out of the sediment. Under these conditions, the influence of animal activity in enhancing these rates become increasingly important with animal density (Forster et al., 2003; Volkenborn et al., 2007). These sedimentary processes could be one possible explanation for the rather abrupt transitions observed between the habitats in the BCA (Figure 4a,c). In this sense, the biological traits are useful in further elaborating the possible causes for some of the observed patterns.

As with the abiotic parameters and macrofauna densities, the most extreme contrasts in the associated functional traits were also found between the two different slopes of the sand waves. Additionally, the majority of the gentle-slope taxa lived superficially in the sediment (<5 cm depth), indicative of the fact that sedimentary organic matter content is significantly lower there. The dominant feeding mode was the downward conveyor (e.g., Terebellidae), which are organisms that predominantly feed at the surface and drag fecal particles into the sediment (Kristensen et al., 2012). A relatively high number of deposit feeders and carnivore-scavenging fauna were also observed on the gentle slope and crest, as was the highly mobile polychaete, *Nephtys* sp., known for its high resiliency to environment stress (Arndt-Sullivan & Schiedek, 1997; Van Lancker et al., 2012). As such, these two habitats are characterized by highly resilient, highly mobile taxa residing and feeding close to the sediment surface. However, the crest was notably different from other habitats only with its relatively high number of surficial modifying organisms; contrary to the gentle slope, the tops of the sand waves contained many more species that were in common with the steep half. This suggests that the crest is actually more of a transition zone that, although it overwhelmingly shares its sediment characteristics with the gentle slope (Table 1), its species composition overlaps with both slopes.

In contrast, the steep slopes were characterized by a large percentage of crawlers and contained the most surficial modifiers. In direct opposition to the more organically poor gentle slope, the steep slope also contained upward conveyors, which feed into the sediment and transport particles toward the surface (Kristensen et al., 2012), thus relying on dissolved and particulate carbon from deeper sediment layers (Clough & Lopez, 1993; Pearson, 2001). Despite having the largest concentration of suspension feeders, notably the bivalves *T. ferruginosa* and the suspension-deposit feeding *F. fabula*, the tubicolous worms were the lowest in proportion in this habitat. Rather, densities of tube-dwelling worms, comprised mostly of Phoronida, were highest in the trough. Despite similar sediment characteristics, the fauna between the trough and steep slope exhibited somewhat less overlap. The deepest burrowers were found in both habitats, along with higher organic matter concentrations and amounts of silty material, indicative of environments where the grain composition and particle quality (e.g., organic matter) are most important for the benthos (Graf, 1992; Pearson, 2001). The disproportionately high biomass and elevated organic matter concentration on the steep slope habitat is an indication of a relatively stable environment with just the right amount of food, so that oxygen depletion is not a detrimental problem (Pearson & Rosenberg, 1977). The lower number of resilient groups are also indicative that the steeper side of the sand waves is somewhat less stressful than the gentle slope and crest, although the low percentage of tubicolous worms also means that this environment is slightly more stressful than the trough. The significantly higher numbers of echinoderms, some of which are active deposit feeders, on the steep slope would suggest this habitat to be more affected by the benthic community (Ziebis et al., 1996; Pearson, 2001), as opposed to the gentle slope that appears to be more physically controlled: the sediment was significantly coarser and the permeability about twice as high on the gentle slope and crest versus the other two habitats (Cheng et al., 2020). The strong physical control is also a probable explanation for the low numbers of sedentary tubicolous worms on the steep slope. Their establishment may be restricted by the destabilizing effect of continuous displacement of sediment both by motile subsurface deposit feeders (Myers, 1977; Pearson, 2001; Rhoads & Young, 1970) and also potential burial by the physical movement of sediment as the sand wave migrates toward the direction of the steep slope (Besio et al., 2004, 2008; Borsje et al., 2014; Van Oyen et al., 2013). Such possible negative effects due to biotic interactions become more pronounced in environments where the physical influences are lessened (Crain & Bertness, 2005; Menge & Sutherland, 1987). On the other hand, the presence of key engineers has also been shown to positively facilitate ecosystem functioning and biodiversity, through the creation of more suitable habitats, thereby increasing the overall habitat heterogeneity (Crain & Bertness, 2006). Hence, the largest differences were observed between the two slopes.

4.2 | Implications and conclusion

Our study demonstrates that significant contrasts in benthic community structure occur over a very small spatial scale (10–100 m) in soft sediment shelves, such as a sand wave environments. In this context, within-habitat conditions such as the position along a single sand wave are the most important determinants of community structure. In spite of the importance attributed to water depth, both at regional and sand wave scales (Baptist et al., 2006; Heip et al., 1992; Künitzer et al., 1992), our results show a much stronger effect from bottom geomorphology. We found the largest differences in most of the measured parameters between the two sides of the Texel sand waves, irrespective of their comparable water depths. Thus, a lower sampling resolution of only the crest and trough would likely have given a totally different observation. Water depth is not a useful indicator for asymmetrical sand wave environments, as it is unable to distinguish between the two sides of the bedforms. Instead, it appears that the specific location (habitat) along the sand wave will have the largest influence over the sedimentary conditions. Despite the fact that the Texel sand waves were overall sandy, all three studies have now demonstrated significant variability in the sediment characteristics, bed roughness, and benthic community composition along the asymmetrical sand waves (Cheng et al., 2020; Damveld et al., 2018). In the case of benthic diversity (e.g., species richness), the Texel sand waves are more resembling the assemblage from the more diverse (and somewhat more muddy) northern region within the Dutch sector.

Although sand waves are ubiquitous throughout the Dutch North Sea, they are predominantly located 20 km or more from the coast given the particular hydrodynamic and sedimentological conditions required for these bedforms to develop and persist. But as biological and environmental processes are often closely coupled, further investigations should consider both aspects simultaneously (Snelder et al., 2007). In addition, a higher spatial resolution of sampling is required to be able to fully grasp the interrelations between sedimentology, morphology, benthic community structure, and biogeochemistry of heterogeneous habitats such as dynamic sand wave environments. The use of habitat classification schemes could be a useful predictor for environments that are similar in terms of sedimentary or other physical characteristics, as these rely on the abiotic parameters that are of significance to both physical and biological patterns (Gregr & Bodtker, 2007; Reiss et al., 2010; Roff et al., 2003). Furthermore, a thorough investigation on the specific interactions between the dominant taxon groups and their influence on one another would provide valuable insight on the significance of biotic controls on community structure, relative to other factors (e.g., physical). Based on our data, we have been able to identify at least four distinct habitats (trough, gentle slope, crest, and steep slope), each with a few dominant predictors within an asymmetrical sand wave. Although the transitional zones between habitats were sometimes rather abrupt, we believe that our findings will provide a basis for a full understanding on the benthic ecological functioning of sand waves.

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CONFLICT OF INTEREST

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

AUTHOR CONTRIBUTIONS

Chiu H. Cheng: Conceptualization, Methodology, Investigation, Formal analysis, Visualization, Writing—Original Draft, Writing—Review and Editing, and Project administration. **Bas W. Borsje:** Conceptualization, Writing—Review and Editing, and Supervision. **Olivier Beauchard:** Methodology, Formal analysis, Visualization, Writing—Original Draft, Writing—Review and Editing, Software, and Resources. **Sarah O'Flynn:** Methodology, Investigation, Writing—Review and Editing, and Resources. **Tom Ysebaert:** Resources, Writing—Review and Editing, and Funding acquisition. **Karline Soetaert:** Conceptualization, Methodology, Investigation, Formal analysis, Visualization, Writing—Review and Editing, Supervision, Project administration, and Funding acquisition.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study will be made openly available in the 4TU. ResearchData repository at https://doi.org/10.4121/14152187.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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