



Linking the morphology and ecology of subtidal soft-bottom marine benthic habitats: A novel multiscale approach

Sebastiaan Mestdagh^{a,*}, Alireza Amiri-Simkooei^{b,c,1}, Karin J. van der Reijden^d, Leo Koop^b, Sarah O'Flynn^a, Mirjam Snellen^b, Christiaan Van Sluis^e, Laura L. Govers^{d,f}, Dick G. Simons^b, Peter M.J. Herman^{g,h}, Han Olf^d, Tom Ysebaert^{a,i}

^a Department of Estuarine and Delta Systems, NIOZ Royal Netherlands Institute for Sea Research and Utrecht University, P.O. Box 140, 4400 AC, Yerseke, the Netherlands

^b Acoustics Group, Faculty of Aerospace Engineering, Delft University of Technology, 2629 HS, Delft, the Netherlands

^c Department of Geomatics Engineering, Faculty of Civil Engineering and Transportation, University of Isfahan, 81746-73441, Isfahan, Iran

^d Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences, University of Groningen, P.O. Box 11103, 9700 CC, Groningen, the Netherlands

^e The North Sea Foundation, P.O. Box 1578, 3500 BN, Utrecht, the Netherlands

^f Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research and Utrecht University, P.O. Box 59, 1790 AB, Den Burg, the Netherlands

^g DELTARES, P.O. Box 177, 2600 MH, Delft, the Netherlands

^h Delft University of Technology, Hydraulic Engineering, 2629 HS, Delft, the Netherlands

ⁱ Wageningen Marine Research, Wageningen University and Research, P.O. Box 77, 4400, AB, Yerseke, the Netherlands

ARTICLE INFO

Keywords:

Sandbanks
Seafloor morphology
Sand waves
Macrobenthos
Multibeam sonar
Video transect

ABSTRACT

High-resolution surveying techniques of subtidal soft-bottom seafloor habitats show higher small-scale variation in topography and sediment type than previously thought, but the ecological relevance of this variation remains unclear. In addition, high-resolution surveys of benthic fauna show a large spatial variability in community composition, but this has yet poorly been linked to seafloor morphology and sediment composition. For instance, on soft-bottom coastal shelves, hydrodynamic forces from winds and tidal currents can cause nested multiscale morphological features ranging from metre-scale (mega)ripples, to sand waves and kilometre-scale linear sandbanks. This multiscale habitat heterogeneity is generally disregarded in the ecological assessments of benthic habitats. We therefore developed and tested a novel multiscale assessment toolbox that combines standard bathymetry, multibeam backscatter classification, video surveying of epibenthos and box core samples of sediment and macrobenthos. In a study on the Brown Bank, a sandbank in the southern North Sea, we found that these methods are greatly complementary and allow for more detail in the interpretation of benthic surveys. Acoustic and video data characterised the seafloor surface and subsurface, and macrobenthos communities were found to be structured by both sandbank and sand wave topography. We found indications that acoustic techniques can be used to determine the location of epibenthic reefs. The multiscale assessment toolbox furthermore allows formulating recommendations for conservation management related to the impact of sea floor disturbances through dredging and trawling.

1. Introduction

Subtidal soft-sediment beds form the most widespread benthic habitat type on earth and result from the interplay of geological, physical and biological drivers (Snelgrove, 1994; Zeiler et al., 2008). When

occurring within the depth range affected by hydrodynamic activity from wind and currents (e.g. < 50 m deep on coastal shelves), these sediment beds form clear, multiscale nested structures, such as sandbanks, sand waves, or (mega)ripples (Mazières et al., 2015; Passchier and Kleinhans, 2005). Consequently, heterogeneous seafloor landscapes

* Corresponding author.

E-mail addresses: sebastiaan.mestdagh@nioz.nl (S. Mestdagh), a.amirisimkooei@tudelft.nl (A. Amiri-Simkooei), k.j.van.der.reijden@rug.nl (K.J. van der Reijden), l.koop@tudelft.nl (L. Koop), sarah.oflynn@nioz.nl (S. O'Flynn), m.snellen@tudelft.nl (M. Snellen), c.vansluis@noordzee.nl (C. Van Sluis), l.l.govers@rug.nl (L.L. Govers), d.g.simons@tudelft.nl (D.G. Simons), peter.herman@deltares.nl (P.M.J. Herman), h.olff@rug.nl (H. Olf), tom.ysebaert@nioz.nl (T. Ysebaert).

¹ Shared first authorship.

<https://doi.org/10.1016/j.ecss.2020.106687>

Received 9 October 2019; Received in revised form 14 January 2020; Accepted 1 March 2020

Available online 5 March 2020

0272-7714/© 2020 The Authors.

Published by Elsevier Ltd.

This is an open access article under the CC BY-NC-ND license

(<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

are created, in which topographic features shape soft-sediment habitat diversity with respect to sediment type and hydrodynamic exposure. This impact of topography on habitat heterogeneity is additionally complemented by variations in the physico-chemical composition of the sediment. In a sandbank system, for example, a clear sediment distribution can be distinguished, with generally finer and carbonate-poorer sediments in the troughs than on the crest (Heathershaw and Codd, 1986; Trentesaux et al., 1994). Habitat variation resulting from this physico-chemical heterogeneity of the seafloor creates important variation in habitat conditions for benthic fauna. Spatial heterogeneity therefore influences important ecosystem features at various scales, including species diversity, density and biomass, community composition, and several ecosystem processes (García-Charton et al., 2004; Lovett et al., 2006). Classic ecology theory states that more heterogeneous habitats support more species per unit area (MacArthur and Wilson, 1967; Tilman, 1982). In marine ecosystems, for example, macrobenthic communities tend to be richer, denser, and different in species composition in troughs than on crests of sandbanks (van Dijk et al., 2012), but also of sand waves (Damveld et al., 2018) and small-scale ripples (Ramey et al., 2009).

In terms of biodiversity, underlying gradients in the physical habitat template can be greatly amplified by biological mechanisms, especially where organisms modifying their physical habitat ('ecosystem engineers' *sensu* Jones et al., 1994) play a decisive role. Such abrupt biogenic landscape boundaries are well known from coral reefs, but also from intertidal habitats where several autogenic ecosystem engineers form complex three-dimensional structures, e.g. at the boundary of vegetated and non-vegetated tidal flats or seagrass meadows (Koch et al., 2006; Temmerman et al., 2005), or in the vicinity of oyster reefs and other bivalve beds (van der Zee et al., 2012; Walles et al., 2015). Through density-dependent feedbacks, ecosystem engineers can buffer the impact of physical forces, although their occurrence is generally limited where these physical forces exceed critical thresholds. In heavily trawled subtidal soft-sediment areas with high substrate mobility, such as sand wave-dominated sediments, their presence seems limited but not absent (Houziaux et al., 2008). Some reef-forming organisms, such as tube worms, may occur in sandbank troughs, where food and suspended sediment needed to build their tubes are sufficiently present (van der Reijden et al., 2019; Van Lancker et al., 2012). The presence of these reefs induces high local biodiversity, sustained by increased local habitat heterogeneity, physical shelter and better food supply (Dubois et al., 2002; Gravina et al., 2018; Rabaut et al., 2007).

Anthropogenic physical disturbance, e.g. bottom trawl fisheries, tends to homogenise soft-bottom sediments by removing smaller-scale habitat heterogeneity in subtidal soft sediments, jeopardising their structure, function and biodiversity (McConnaughey et al., 2000; Thrush and Dayton, 2002). Epibenthos is particularly vulnerable to this influence (Jenkins et al., 2015; van der Reijden et al., 2019), but infaunal organisms are also affected, resulting in a shift of benthic communities towards a dominance of shorter-lived species (Rijnsdorp et al., 2018; Sciberras et al., 2018). Given the high prevalence and intensity of demersal fisheries in shallow coastal seas such as the North Sea (Amoroso et al., 2018; Eigaard et al., 2017; van der Reijden et al., 2018), benthic surveys may not be sufficiently able to reveal the biodiversity potential of many benthic (sub)habitats created by the interplay between hydrodynamic and biological forces. An approach that resolves the underlying physical gradients and evaluates both the potential of this template for biogenic self-reinforcing biodiversity development, and vulnerability/sensitivity to disturbance, is therefore needed.

The most important constraint for biodiversity-oriented benthic surveys is the trade-off between extent and 'grain' (resolution in space and time, and in terms of variables estimated) of the different observational methods. As sampling is often costly and time-consuming, and areas needing coverage are large, a balance between extent and resolution needs to be found (Bates et al., 2007; Bennett et al., 2014). With respect to the identification of the physical habitat template, a very

promising approach is the use of multibeam echo-sounding (MBES). Especially when the full information in the returning acoustic signals (including backscatter intensity) is used, this acoustic technique allows for a detailed characterisation of the seafloor bathymetry, but can also give information about the sediment type variation of the seafloor (De Moustier and Matsumoto, 1993; Hellequin et al., 2003). However, the method does not give direct information on the species composition of benthic assemblages (Brown et al., 2011). *In situ* sampling remains necessary to link topography to seafloor ecology. To map seafloor communities, multibeam data can be combined with camera surveying, such as video transects, photos of the seafloor by landing frames or sediment profile imaging (SPI camera; Rhoads and Cande, 1971), or by box core samples. Between these techniques, there is also a trade-off between the area covered per unit effort, and taxonomic resolution of the biodiversity surveys. An optimal combination of several techniques is likely the best compromise between these approaches.

In this study, we combined MBES, video, photographic (SPI) and box core sampling of the seafloor macrobenthos communities in a dynamic area in the southern North Sea. We tested how the combination of these techniques can be used to accurately link biodiversity to seafloor morphology and explored if it enables us to upscale locally sampled biodiversity patterns to the wider seafloor landscape. Since different seafloor morphologies can offer different substrate characteristics and varying food availability to the benthic fauna, we also explored the relationships between benthic macrofauna abundance and biodiversity, and sediment grain size and organic matter quantity and biochemical composition. The aim of this study is to quantify the correlation between the outcomes of the different approaches and to generalise this information in the design of optimal survey approaches for larger areas of the North Sea.

2. Material and methods

2.1. Study area

This study focused on the Brown Bank, a large sandbank with a height difference of about 26 m between crest and trough, belonging to the north-south oriented Dutch Banks in the southern North Sea (Fig. 1). The sandbank is located nearly halfway between the Netherlands and the United Kingdom, at about 85 km from the Dutch coast. The seafloor in this region additionally forms smaller-scale sand waves that are roughly east-west oriented, with wavelengths of about 200 m and heights of 5 m, and smaller megaripples, with wavelengths and heights of about 10 m and 0.1 m, respectively. Both sand waves and megaripples migrate over the seafloor, at rates in the order of several metres per year for sand waves and within weeks or even hours for megaripples (Knaapen, 2009, 2005; Koop et al., 2019). The area is heavily fished by bottom trawlers, especially the troughs between the large sandbanks (van der Reijden et al., 2018). The sampling took place from 26 October till 5 November 2017, during a campaign on board RV *Pelagia*.

2.2. Multibeam echo sounding

A hull-mounted Kongsberg EM302 MBES (Kongsberg Maritime, Kongsberg, Norway) with a central frequency of 30 kHz was deployed during the sampling campaign. The MBES operated with 432 beams, a swath opening angle of 130°, and across and along track beam opening angles of two and one degrees, respectively. Bathymetry and backscatter were logged using the Kongsberg Seafloor Information System software.

The data were cleaned in Qimera, exported using Qinsky (Quality Positioning Services, Zeist, the Netherlands), and further processed in MatLab 2018b. Steep seafloor slopes were corrected and a Bayesian classification method was performed on the backscatter data, yielding four acoustic classes for the survey area (Alevizos et al., 2015; Amiri-Simkooei et al., 2009; Koop et al., 2019; Simons and Snellen, 2009). From the backscatter data, sediment median grain size M_z , surface

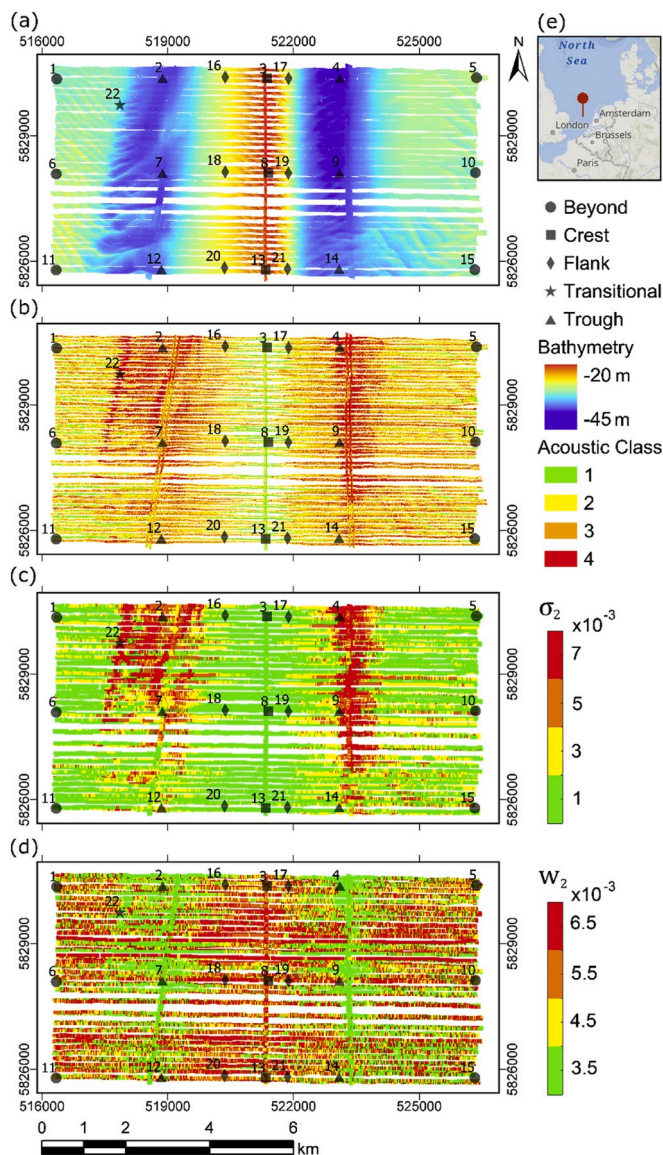


Fig. 1. Location of the 22 sampling stations on and around the Brown Bank, with background colour indicating (a) bathymetry, (b) backscatter-based acoustic classes, (c) volume scattering (σ_2) and (d) surface roughness (w_2). The inset (e) shows the location of the Brown Bank in the southern North Sea. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

roughness w_2 and volume scattering σ_2 were calculated, whereby the latter two variables describe the backscatter signal caused by seafloor surface roughness and by heterogeneities underneath the sediment surface, respectively (Amiri-Simkooei et al., 2019; Collier and Brown, 2005; Jackson and Briggs, 1992). Bathymetry was used to calculate slope and the Bathymetric Position Index (BPI) for each pixel, which represents the average height difference between that pixel and its surroundings within a pre-defined radius. We used BPI2000 (with a 2000 m radius) as a measure for sandbank topography, BPI200 for sand waves and BPI10 for megaripples.

2.3. Box core samples

After inspection of the seafloor bathymetry based on the MBES, 22 stations on and around the Brown Bank were selected for sampling. Along three transects (north, middle, south), stations were chosen on the sandbank crest and flanks, in the troughs and beyond the troughs in sand

wave-dominated areas that form gentle slopes of the next sandbanks. Based on a real-time observed deviating pattern in the acoustic data, an additional transitional station (station 22) was sampled, at the western edge of the western trough (Fig. 1). The sampled stations were classified according to their topographic position: 'Crest', 'Flank', 'Trough', 'Transitional' and 'Beyond', the last of which refers to the sand wave-dominated area beyond the troughs of the Brown Bank. At each station, three replicate box core samples were taken with a box corer (30 cm internal diameter). Beyond the eastern trough of the Brown Bank, two stations were located in a sand wave trough (stations 10 and 15) and one (station 5) on a crest, whereas two stations were located on a stoss-side flank (stations 6 and 11) and one (station 1) in a trough of a sand wave beyond the western trough of the sandbank.

From each box core sample, sediment subsamples were taken with a 50 ml syringe and immediately stored at -20°C before processing. After at least four days of freeze drying, these subsamples were analysed for granulometry, chlorophyll *a* concentration, total organic carbon (TOC) and total nitrogen (TN). Granulometry was determined by sieving the samples over a 4 mm, 2 mm and 1 mm mesh and analysing the smallest fraction by laser diffraction with a Malvern Mastersizer 2000 (Malvern Instruments, Worcestershire, UK). The larger sediment fractions were weighed, and mass percentages were calculated for each separate fraction. However, since these mass percentages were negligible (less than 2% of the total mass in most samples), the coarser fractions were discarded for further analysis. After extraction in a bullet blender with 90% acetone, chlorophyll *a* was analysed using a Specord 210 spectrophotometer (Analytik Jena, Jena, Germany). TOC and TN were analysed according to the Dumas method (Nieuwenhuize et al., 1994), using a Thermo Flash 2000 Element Analyser (Thermo Fisher Scientific, Waltham, Massachusetts, USA).

The remaining sediment was sieved over a 0.5 mm mesh to extract the macrobenthos. Animals were fixed in 4–6% formalin and transported to the laboratory, where they were counted and identified to the lowest possible taxonomic level. For each sample, densities, species richness (*S*) and Pielou's evenness (*J'*) were calculated. Furthermore, functional groups were defined based on combinations of sediment reworking mode (E: epifauna, S: surficial modifiers, C: conveyor-belt feeders, B: biodiffusors, R: regenerators), and motility in the sediment (A: in a fixed tube; B: sessile, but not in a tube; C: slow movement through the sediment; D: free movement through a burrow system; Queirós et al., 2013; Solan et al., 2004).

2.4. Sediment profile imaging

A Sediment Image Profiler (SPI) was used to determine the subsurface seabed structure. The SPI consists of a galvanised frame with a camera-comprising prism, which protrudes the seafloor when lowered onto the seabed (Rhoads and Cande, 1971). The SPI was lowered three times at each, except the transitional, station. At each drop, two pictures were taken, resulting in 6 pictures per station. The penetration depth was measured, the presence of shell fragments was classified (0: no shell fragments; 1: few shell fragments; 2: medium shell fragments; 3: many shell fragments), and the dominant sediment type was identified (Sand or Mud).

2.5. Video transects

Videos of the seabed were collected using a towed video camera frame, as described in Koop et al. (2019). This aluminium frame was equipped with a remotely operated video camera (Kongsberg OE14-522A-0009 Colour HD Pan), lights (Fisheye FIX NEO 1000DX SW II LED), and lasers (Z-Bolt, SCUBA-II green) for scaling. Its approximate height above the seabed was constantly checked using live view from the camera. The length of the towing cable was adjusted to maintain the desired height if needed. During video operations, the vessel had a speed of ± 0.1 m/s, with the camera towed at approximately 0.5 m above the

seafloor.

Video transects were performed at 10 stations, in the crest and both troughs, and the transitional station (see Supplement Fig. 1). Two transects were performed for each except the transitional station. Validity and superficial landscape type were deduced from the video footage, as well as shifts between landscape types and the number of observed organisms. The observed species were identified to the lowest taxonomic level possible. The horizontal geographic position of the camera was deduced from a time match with interpolated GPS positions of the vessel, which were recorded every 30 s. For each transect, the surveyed area was determined as the summed surface of grid cells with camera presence in a 0.50×0.50 m grid. The number of individuals of each species could hence be converted to densities (m^{-2}) per transect. The number of switches in landscape type was determined as an indicator of small-scale habitat heterogeneity. For this, the number of landscape switches was divided by the length of the transect, which was determined as the sum of distances between valid recordings.

2.6. Statistical analysis

All variables concerning macrobenthos density and diversity, and sediment properties were analysed through a Kruskal-Wallis test, using the topographic position (TP) on or around the sandbank as the predictor with five levels ('Crest', 'Flank', 'Trough', 'Transitional', 'Beyond'), followed by a Dunn test for pairwise contrasts. In the 'Beyond' TP, a Mann Whitney *U* Test was conducted with the same properties, to discern between sand wave flanks/crests and troughs. The composition of macrobenthos communities in the different TPs was analysed with a one-factor PERMANOVA on species densities and functional group densities, using the function *adonis()* in the R package *vegan* (Oksanen et al., 2017). Homogeneity of dispersions was tested with function *betadisper()* in the same package. For 'Trough', 'Flank' and 'Beyond', one-factor PERMANOVA analyses were conducted to reveal differences between the eastern and western side of the Brown Bank. The data were further explored through Non-metric MultiDimensional Scaling (NMDS), on which the topographic position, orientation and location of sand waves were indicated. SIMPER analyses were performed to reveal the most discriminating species or functional groups between the TPs.

The penetration depth for the SPI pictures was tested using a linear mixed model (LMM), with topographic position as explanatory and station as random variable. Log likelihood ratio was determined between this model and a null model with only the random effect of station included. For both the organism density and the small-scale heterogeneity based on video data, a similar approach was taken.

Acoustic data derived from the MBES and other environmental data were linked to macrobenthos community data via redundancy analysis (RDA). Both species densities and functional group densities were tested. A backward stepwise selection was performed to select significant variables from the full set of MBES data (M_z , w_2 , σ_2 , slope, backscatter, bathymetry, BPI2000, BPI200, BPI10), as well as TOC, TN and chlorophyll *a* content for the RDA model.

All analyses were performed in the open source statistical software R (R Core Team, 2018). Values are represented as mean \pm standard deviation.

3. Results

3.1. Acoustic characterisation of the seafloor

Bathymetric mapping clearly indicated the presence of the sandbank, flanked east and west by troughs, and a sand wave-dominated region beyond the troughs. The bathymetric features can also be distinguished when using backscatter classes or either surface roughness w_2 or volume scattering σ_2 for mapping, with generally higher backscatter values in the troughs and lower on the crests. Backscatter shows similar patterns

as σ_2 , while w_2 gives an inverse pattern, with lower values in the troughs and higher on the crest (Fig. 1).

3.2. Abiotic properties of the sandbank sediments

The median grain size and mud content of the sediment were found to differ significantly between different TPs, with the 'Transitional' differing most from the other TPs (Table 1). While grain sizes and mud content in the 'Transitional' reached values of $43.33 \pm 25.93 \mu m$ and $60.13 \pm 15.48\%$, respectively, median grain size in the other TPs ranged from $294.65 \pm 12.97 \mu m$ ('Flank') to $314.65 \pm 16.24 \mu m$ ('Crest'), and mud content from $0 \pm 0\%$ ('Crest' and 'Flank') to 1.63 ± 3.31 ('Trough').

TOC differed significantly between nearly all TPs. Only the 'Flank' and 'Beyond', and the 'Trough' and 'Transitional' were similar. TOC was highest in the 'Transitional' ($0.59 \pm 0.19\%$) and lowest on the 'Crest' ($1.17 \pm 0.32 \times 10^{-2}\%$). TN values were significantly different between the 'Transitional' and other TPs, and between the 'Trough' and other TPs, but not between 'Transitional' and 'Trough'. Values were lowest on the 'Crest' ($4.67 \pm 3.16 \times 10^{-3}\%$) and highest in the 'Transitional' ($6.12 \pm 1.36 \times 10^{-2}\%$). Chlorophyll *a* content showed significant and similar patterns, with highest values in the 'Trough' ($0.51 \pm 0.27 \mu g g^{-1}$) and lowest on the 'Crest' ($0.08 \pm 0.02 \mu g g^{-1}$). Of the sediment properties, only chlorophyll *a* content was found significantly different between the flanks and troughs of sand waves within the 'Beyond', with higher values in the troughs than on the flanks (Table 1).

3.3. Subsurface seabed structure

At two stations, only four usable pictures were obtained due to malfunctioning of the SPI. The average penetration depth was 6.3 ± 2.9 cm, with 39 pictures having a penetration depth of <5 cm. Penetration depth was much larger on the crest (11.5 ± 2.9 cm) than at the other locations (5.6 ± 2.1 cm) (log likelihood ratio of LMM: -6.8). The amount of shell fragments was higher in the troughs compared to the crest locations, as crest pictures were all classified as no shell fragments (class 0), while the trough pictures showed the highest percentages of class 1 and 2 (medium and many shell fragments, respectively).

Table 1

Kruskal-Wallis and Dunn tests for significant differences of abiotic (median grain size, mud content, TOC: Total Organic Carbon, TN: Total Nitrogen, chlorophyll *a* content) and biotic variables (*S*: Species richness, *J'*: Pielou's evenness) between the various Brown Bank topographic positions, and p-values of the Mann-Whitney *U* test (MWU) to discern between sand wave flanks and troughs. Bey: Beyond; Cre: Crest; Fla: Flank; Tra: Transitional; Tro: Trough.

Variable	Kruskal-Wallis Test		Significant pairwise contrasts ($\alpha = 0.05$)	MWU
	χ^2	p		
Median grain size	16.60	<0.001	Bey-Fla, Bey-Tra, Cre-Fla, Cre-Tra, Fla-Tra, Tra-Tro	0.387
Mud content	31.10	<0.001	Bey-Tra, Cre-Tra, Fla-Tra, Fla-Tro, Tra-Tro	0.374
TOC	45.90	<0.001	Bey-Cre, Bey-Tra, Bey-Tro, Cre-Fla, Cre-Tra, Cre-Tro, Fla-Tra, Fla-Tro	0.058
TN	27.38	<0.001	Bey-Tra, Bey-Tro, Cre-Tra, Cre-Tro, Fla-Tra, Fla-Tro	0.627
Chlorophyll <i>a</i>	42.22	<0.001	Bey-Cre, Bey-Tro, Cre-Fla, Cre-Tra, Cre-Tro, Fla-Tra, Fla-Tro	<0.001
<i>S</i>	25.78	<0.001	Bey-Cre, Bey-Tra, Bey-Tro, Cre-Fla, Cre-Tra, Cre-Tro, Fla-Tra, Fla-Tro	0.033
<i>J'</i>	2.86	0.580		0.114
Total density	23.31	<0.001	Bey-Cre, Bey-Tro, Cre-Fla, Cre-Tra, Cre-Tro, Fla-Tra, Fla-Tro	0.667

3.4. Video transects

A total of 1813 individuals of 16 species were observed, over a total observed area of 1358 m². The most recorded species was the starfish *Asterias rubens* (1378 individuals), followed by Ophiuroidea brittle stars (256 ind.) and the hermit crab *Pagurus bernhardus* (65 ind.). Compared to the crest (0.128 ± 0.057), the troughs (East: 3.079 ± 4.502; West: 0.770 ± 0.298) had higher densities of organisms (log likelihood ratio LMM: -4.9). Moreover, the troughs (East: 3.463 ± 2.876; West: 5.315 ± 3.183) showed 3 to 5 habitat type changes per 100 m transect, while the crest showed none (log likelihood ratio LMM: -4.9). Crest transects only showed sandy sediment with hardly any shell fragments, while all other stations alternated between sandy sediments with shell fragments and sandy sediments with shell fragments and incidental large stones (see Supplement Fig. 1). Sandy sediments with shell fragments, incidental stones and *Sabellaria* reef fragments (*Sabellaria* landscape) were observed in the northern station in the eastern trough (station 4) and the middle station in the western trough (station 7). Moreover, the transitional station (station 22) showed some *Sabellaria* habitat, but also the unique “sand with clay” and “sand with clay and incidental stones” habitats.

3.5. Macrobenthos communities in the different topographic positions

A total of 129 different taxa, divided over 9 phyla, was observed (see Supplement Table 1). Overall, communities were mostly dominated by mobile hooded shrimp (cumaceans) and amphipods, whereas less mobile species, among which phoronids, sessile polychaetes and bivalves, reached higher densities in the ‘Trough’ and the ‘Transitional’ (see Supplement Table 2). Here, individuals of the reef-building Ross worm (*Sabellaria spinulosa*) were also found. Community composition was determined by the TPs within the Brown Bank environment, as indicated by the PERMANOVA test (Table 2). Significant differences between habitats were found for all pairwise contrasts, except between the ‘Flank’ and the ‘Beyond’ and between the ‘Trough’ and the ‘Transitional’. Significant differences between the eastern and western side were found within the ‘Beyond’ and between the two flanks of the Brown Bank. Fourteen different functional groups of macrobenthos, based on sediment reworking mode and motility, were identified in our dataset (see Supplement Table 1). Functional group composition also differed significantly among TPs (Table 2). While surficial modifiers that slowly move through the sediment (SC) were the dominant functional group in all TPs, biodiffusers (BC) reached similar densities in the sandbank troughs and on the flanks. Functional community compositions in the ‘Trough’ and ‘Flank’ were found significantly different from the other TPs, except from the ‘Beyond’. However, the northernmost station of the eastern trough (station 4) was located far outside the point cloud on the NMDS plot, and after removal of this point, no significant effect of sandbank region was found in the PERMANOVA test (Table 2). The NMDS plot with the taxonomical community compositions show

Table 2

PERMANOVA results, testing taxonomical and functional macrofauna community composition for significant differences between topographic positions (TP), and testing between eastern and western troughs, flanks and beyond troughs. P: p-value for the PERMANOVA test; P (disp): p-value for the multivariate dispersion of variances. The asterisk (*) represents the results of the test after removal of the outlying station 4.

Sandbank TP	Pseudo-F	P	P (disp)
Taxonomical	4.54	<0.001	0.096
Functional	3.76	<0.001	0.287
Functional*	1.77	0.055	0.363
East-West			
Trough	1.68	0.095	0.099
Flank	3.76	<0.001	0.720
Beyond	2.96	0.002	0.913

that within the ‘Beyond’, both functional and taxonomical community composition from the troughs and crests of sand waves share relative similarities with the sandbank trough and crest communities, respectively (Fig. 2).

The species richness was lowest with 9.44 ± 3.50 species per sample on the ‘Crest’ and highest with 28 ± 9.54 species in the ‘Transitional’, and showed significant differences between all TPs, except between the ‘Flank’ and ‘Beyond’ and between the ‘Trough’ and the ‘Transitional’. Pielou’s evenness ranged from 0.79 ± 0.08 in the ‘Trough’ to 0.84 ± 0.09 on the ‘Crest’ and did not differ significantly among TPs (Table 1). In the ‘Beyond’, species richness, but not Pielou’s evenness, was found significantly different between sand wave crests and troughs. Total densities were lowest on the ‘Crest’ (380.40 ± 224.52 individuals/m²) and highest in the ‘Trough’ and ‘Transitional’ (2092.99 ± 2834.49 and 1872.13 ± 1092.39 individuals/m², respectively). Densities on the ‘Crest’ were significantly lower than all other TPs and densities in the ‘Trough’ significantly higher than all others except the ‘Transitional’.

The SIMPER analysis revealed that the most discriminating species between TPs were hooded shrimp (*Monopseudocuma gilsoni*), horseshoe worms (*Phoronis* sp.) and Ross worms (*Sabellaria spinulosa*) (see Supplement Table 3). *M. gilsoni* was the most discriminating species when comparing most TPs with each other. *Phoronis* sp. was the most important discriminator between ‘Beyond’ and ‘Transitional’, ‘Crest’ and ‘Transitional’ and ‘Flank’ and ‘Transitional’, while *S. spinulosa* was the most discriminating species between the ‘Trough’ and ‘Transitional’. The most discriminating functional group for most pairs of TPs was the group of the surficial modifiers that slowly move through the sediment (SC), a group that encompasses the abundant *M. gilsoni*. Of the significantly different TPs, we found that this group was also the most important discriminator between the ‘Trough’ and ‘Flank’, but sessile surficial modifiers (CB) between the ‘Crest’ and ‘Flank’ and surficial modifiers in a fixed tube (SA) between the ‘Flank’ and ‘Transitional’.

3.6. Integration of the different methods

The video, SPI footage and MBES data show similar features, with the more topographically diverse seafloor habitats outside the sandbank crest corresponding with a higher backscatter signal. For the RDA model linking acoustic and macrobenthos data, the stepwise selection procedure selected TOC, σ_2 and bathymetry as contributing significantly to the variation in macrobenthos (taxonomic) community structure based on densities. The model explained 46.7% of the total variation in the data, with the first two ordination axes explaining 28.6% and 11.9%, respectively. Bathymetry mostly separated the macrobenthos communities in the different topographic positions from each other, as well as sand wave flanks/crests from the sand wave troughs in the ‘Beyond’ TP. TOC and σ_2 mostly separated the majority of the stations from the ‘Transitional’ station and the ‘Trough’ station where video footage showed a high *Sabellaria* presence (Fig. 3a). For the RDA model based on functional groups, σ_2 and backscatter were selected as significant contributors to the variation in community structure, mostly separating the ‘Trough’ and ‘Transitional’ stations, as well as ‘Beyond’ stations in sand wave troughs, from the others (Fig. 3b). This model explained 31.1% of the total variation in the data, with the first two ordination axes explaining 23.7% and 7.3%, respectively.

4. Discussion

4.1. Linking data from multiscale sampling methods

The observation of stones and shell fragments in the troughs from both video and SPI footage and the MBES data, corresponds to earlier findings at the Brown Bank and other sandbanks in the southern North Sea (Bellec et al., 2010; Koop et al., 2019). Houziaux et al. (2011) argued that intensive bottom trawling in the twentieth century probably covered these coarse materials by and mixed them with sand. The

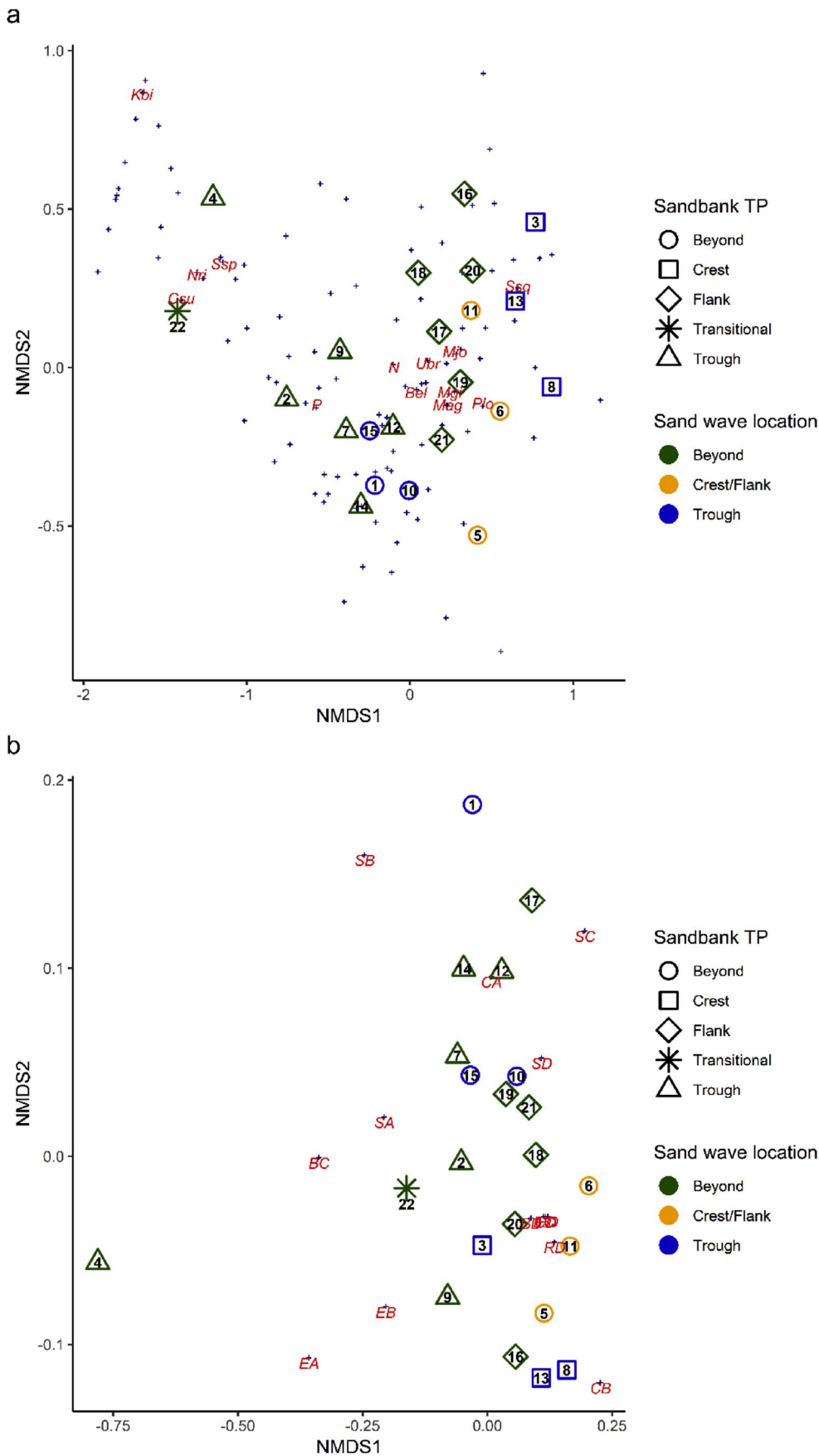


Fig. 2. NMDS plots based on (a) taxonomical composition of the macrobenthic communities, with indication of the species that contributed more than 5% to the dissimilarity between topographic positions (TP) in the SIMPER analysis (*Bel*: *Bathyporeia elegans*; *Csu*: *Callianassa subterranea*; *Kbi*: *Kurtiella bidentata*; *Mag*: *Megaluropus agilis*; *Mgi*: *Monopseudocuma gilsoni*; *Mjo*: *Magelona johnstoni*; *N*: Nemertea; *Nri*: *Nephasoma rimicola*; *P*: *Phoronis* sp.; *Plo*: *Pseudocuma longicorne*; *Ssp*: *Sabellaria spinulosa*; *Ssq*: *Scolecipis squamata*; *Ubr*: *Urothoe brevicornis*) and (b) functional composition of the macrobenthos communities, with functional groups based on sediment reworking mode (E: epifauna, S: surficial modifiers, C: conveyor-belt feeders, B: biodiffusers, R: regenerators), and motility in the sediment (A: in a fixed tube; B: sessile, but not in a tube; C: slow movement through the sediment; D: free movement through a burrow system).

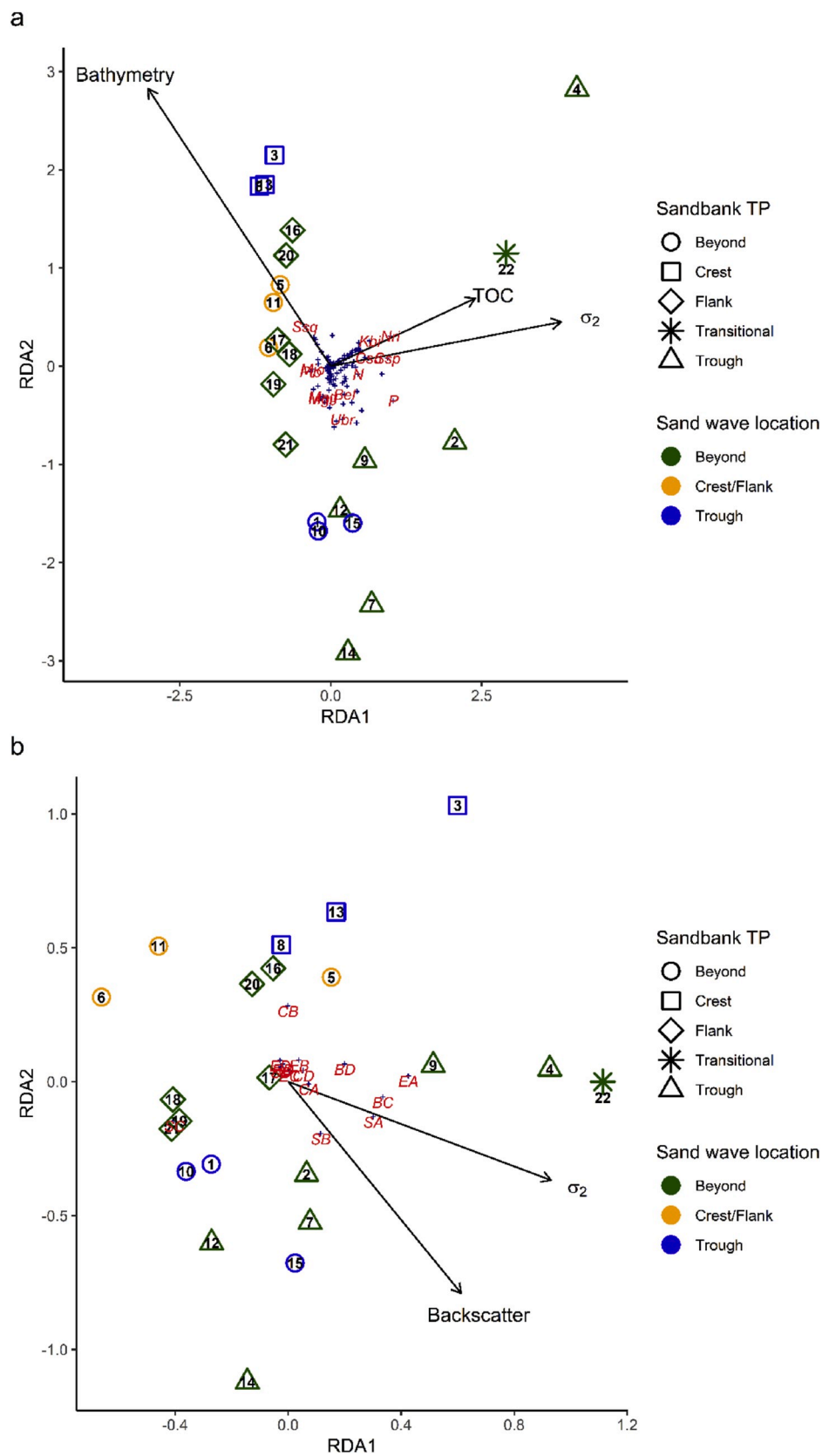


Fig. 3. RDA plots based on (a) taxonomical and (b) functional composition of the macrobenthos communities, with indication of the environmental variables that contribute significantly to the variation and species/functional groups as in Fig. 2. TOC: Total Organic Carbon; Backscatter: Backscatter intensity; σ_2 : Volume scattering.

resulting mixed sediment beds explain the higher volume scattering observed in the sandbank troughs. The relatively low surface roughness on the other hand, suggests a smoother sediment surface in the troughs than elsewhere, possibly due to a relative lack of sand ripples caused by lower hydrodynamic conditions (Amiri-Simkooei et al., 2019).

Macrobenthic community compositions appear to be largely determined by topographic position (as determined by hydrodynamics), with higher biodiversity in the sandbank troughs than on the crest, confirming earlier research (Ellis et al., 2011; van Dijk et al., 2012). Although our communities beyond the Brown Bank troughs were also separated according to their location within sand waves, this smaller-scale separation between communities was not significant. On the other hand, differences between the eastern and western 'Beyond' TP may have been caused by different locations on the sand waves. Note, however, that sand waves were mainly abundant beyond the Brown Bank and its troughs and were therefore only sampled in a small subset of all stations. Moreover, sand wave samples outside troughs were not always taken exactly on a crest, but often on stoss-side flanks, which are affected by the currents, just like crests. Yet, the separation of communities according to their occurrence in either the trough of a sand wave or on its flank, and their relative similarities to those of the corresponding sandbank TPs, indicates that the processes shaping benthic communities operate similarly on different spatial scales. The higher biodiversity in troughs of different scales has been associated with a higher organic matter or mud content (Damveld et al., 2018; Ramey et al., 2009; van Dijk et al., 2012). However, our communities from the sand wave-dominated areas were hardly separated based on their organic matter content (TOC), and we could only find this distinction in sediment properties for the large-scale sandbank. We therefore suggest that – next to sediment properties – physical stress caused by the dynamics of water and sediment is an important factor in determining which species will dominate communities in sand wave environments.

4.2. *Sabellaria* reefs and the impact of bottom trawling

Our findings supported earlier observations of *Sabellaria spinulosa* reef fragments in the troughs around the Brown Bank (van der Reijden et al., 2019). However, analysis of the video and box core data did not always lead to the same conclusions. At the transitional station, high abundances of individual *Sabellaria* worms were found in the box cores, whereas the video showed only few reef fragments. Likewise, in the northernmost station in the western trough one box core sample contained *Sabellaria* worms, but no reef fragments were observed in the video transects. For the northernmost station in the eastern trough and the central station in the western trough, video observations of *Sabellaria* reef fragments did not automatically coincide with frequent presence of *Sabellaria* worms in the box core samples. This indicates that this species has a larger distribution area, but forms reefs solely in specific locations, and its patchy distribution demands a sampling approach covering multiple scales. Our samples suggest that the presence of both *Sabellaria* reefs and individuals stimulates the establishment of diverse and – both taxonomically and functionally – distinct macrobenthos communities. Earlier studies have emphasised the ecological importance of reef-forming benthic species, especially through promoting habitat heterogeneity and organic matter entrapment (Dubois et al., 2002; Godet et al., 2011; Gravina et al., 2018). Interestingly, we show that high abundances of *Sabellaria* individuals might have the same effect. Furthermore, the specific locations where reef fragments were observed appeared to occur in areas characterised by high acoustic volume scattering, suggesting that this parameter can be used to identify potential *Sabellaria* reef locations.

The presence of *Sabellaria* reefs and more diverse and dense macrobenthos communities in the Brown Bank troughs can promote a higher local fish diversity, since several species of demersal fish are known to feed near these reefs (Pearce, 2014). van der Reijden et al. (2018) showed that beam trawl fisheries strongly prefer the Brown Bank

troughs, resulting in intense local fishing. Beam trawling is known to destroy epibenthic structures such as reefs and disrupt endobenthic communities by dragging heavy gear over the seafloor (Bolam et al., 2014; Jones, 1992). This intense trawling is therefore a likely reason why only sparse reefs are known around the Brown Bank, whereas higher amounts of reefs still occur in British waters, where they have enjoyed a longer protection (Gibb et al., 2014; van der Reijden et al., 2019). The macrobenthos communities of the Brown Bank troughs are probably adapted to high disturbance, as the region has already been trawled since the thirteenth, and more intensively since halfway the twentieth century (de Groot, 1984; Frid et al., 2000). As the communities are either influenced by anthropogenic disturbance (bottom trawling in the troughs and lower flanks) or by a higher physical stress (high hydrodynamic regime on the crests and higher parts of the sandbank), their current functional composition lacks a clear distinction. Only where trawling is – probably by chance – relatively limited, for example in topographic "safe sites", both a functionally distinct community and a (small) biogenic reef can form, as observed in the northernmost station of the eastern trough.

4.3. Implications for monitoring

By combining different sampling methods, we obtained a more detailed image of the seafloor than would otherwise be possible. Traditional designs that merely focus on grab or box core samples do not take small-scale heterogeneity of the seafloor into account and extrapolate the findings of sampling points to their direct surroundings. Great care should therefore be taken in the spatial interpolation between samples. Although macrobenthos communities largely corresponded with the Brown Bank morphology, we showed that additional techniques are useful to obtain information about smaller-scale variability. Acoustic data were crucial to identify sand waves, allowing us to compare patterns in community structure on the sandbank and the sand wave scale. Furthermore, video footage revealed that the *Sabellaria* found in the box core samples formed (fragmented) reefs, which occurred only in areas with high volume scattering. Not only can we therefore use these techniques to add detail to our interpretation of seafloor heterogeneity, they may also be useful to delineate regions where biogenic structures can be present, and therefore potentially serve as an important tool in conservation management. The box core samples, in contrast with the other survey techniques, allowed inferring the correlation structure between the occurrence of all species of macrobenthos. This is needed in order to properly evaluate the community effects of features like *Sabellaria* reefs.

5. Conclusion

The combined use of multiple sampling techniques for seafloor and benthos characterisation allowed us to make a detailed interpretation of our findings. As standard sampling schemes tend to inadvertently 'homogenise' the studied region when spatially extrapolating data, we recommend the complementary use of MBES and video footage. This allows for a greater detail of the surveys, allowing us to make predictions about the interlaying seafloor that can potentially serve for conservation 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.

CRedit authorship contribution statement

Sebastiaan Mestdagh: Formal analysis, Writing - original draft, Writing - review & editing. **Alireza Amiri-Simkooei:** Methodology,

Formal analysis, Writing - original draft. **Karin J. van der Reijden:** Conceptualization, Methodology, Writing - review & editing. **Leo Koop:** Conceptualization, Methodology, Writing - review & editing. **Sarah O'Flynn:** Conceptualization, Methodology. **Mirjam Snellen:** Supervision, Writing - review & editing. **Christiaan Van Sluis:** Project administration. **Laura L. Govers:** Supervision, Writing - review & editing. **Dick G. Simons:** Supervision. **Peter M.J. Herman:** Supervision, Writing - review & editing. **Han Olff:** Supervision, Writing - review & editing. **Tom Ysebaert:** Supervision, Writing - review & editing.

Acknowledgments

No conflicts of interest are declared. The authors would like to thank Karlina Soetaert (NIOZ) for organising the cruise and acknowledge Rob Witbaard (NIOZ) for his role as chief scientist during the cruise. The crew of *RV Pelagia* is also acknowledged for their practical assistance on board. Peter van Breugel is thanked for performing the particle size analysis in the NIOZ lab, and Matthew Parsons and Maria Bacelar Martinez for processing of the macrobenthos samples. Finally, the authors acknowledge the Gieskes-Strijbis Fonds for financial support of the DISCLOSE project, within which this research took place.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2020.106687>.

References

- Alevizos, E., Snellen, M., Simons, D.G., Siemes, K., Greinert, J., 2015. Acoustic discrimination of relatively homogeneous fine sediments using Bayesian classification on MBES data. *Mar. Geol.* 370, 31–42. <https://doi.org/10.1016/j.margeo.2015.10.007>.
- Amiri-Simkooei, A., Snellen, M., Simons, D.G., 2009. Riverbed sediment classification using multi-beam echo-sounder backscatter data. *J. Acoust. Soc. Am.* 126, 1724–1738. <https://doi.org/10.1121/1.3205397>.
- Amiri-Simkooei, A.R., Koop, L., van der Reijden, K.J., Snellen, M., Simons, D.G., 2019. Seafloor characterization using multibeam echosounder backscatter data: methodology and results in the North Sea. *Geosciences* 9, 292. <https://doi.org/10.3390/geosciences9070292>.
- Amoroso, R.O., Pitcher, C.R., Rijnsdorp, A.D., McConnaughey, R.A., Parma, A.M., Suuronen, P., Eigaard, O.R., Bastardie, F., Hintzen, N.T., Althaus, F., Baird, S.J., Black, J., Buhl-Mortensen, L., Campbell, A.B., Catarino, R., Collie, J., Cowan, J.H., Durholtz, D., Engstrom, N., Fairweather, T.P., Fock, H.O., Ford, R., Gálvez, P.A., Gerritsen, H., Góngora, M.E., González, J.A., Hiddink, J.G., Hughes, K.M., Intelmann, S.S., Jenkins, C., Jonsson, P., Kainge, P., Kangas, M., Kathena, J.N., Kavadas, S., Leslie, R.W., Lewise, S.G., Lundy, M., Makin, D., Martin, J., Mazor, T., Gonzalez-Mirelis, G., Newman, S.J., Papadopoulou, N., Posen, P.E., Rochester, W., Russco, T., Salal, A., Semmens, J.M., Silvan, C., Tsolos, A., Vanelslander, B., Wakefield, C.B., Wood, B.A., Hilborn, R., Kaiser, M.J., Jennings, S., 2018. Bottom trawl fishing footprints on the world's continental shelves. *Proc. Natl. Acad. Sci. U.S.A.* 115, E10275–E10282. <https://doi.org/10.1073/pnas.1802379115>.
- Bates, C.R., Scott, G., Tobin, M., Thompson, R., 2007. Weighing the costs and benefits of reduced sampling resolution in biomonitoring studies: perspectives from the temperate rocky intertidal. *Biol. Conserv.* 137, 617–625. <https://doi.org/10.1016/j.biocon.2007.03.019>.
- Bellec, V.K., Van Lancker, V., Degrenedele, K., Roche, M., Le Bot, S., 2010. Geo-environmental characterization of the Kwinte bank. *J. Coast. Res. Special Iss.* 63–76. <https://doi.org/10.2112/SI51-006.1>.
- Bennett, J.R., Sisson, D.R., Smol, J.P., Cumming, B.F., Possingham, H.P., Buckley, Y.M., 2014. Optimizing taxonomic resolution and sampling effort to design cost-effective ecological models for environmental assessment. *J. Appl. Ecol.* 51, 1722–1732. <https://doi.org/10.1111/1365-2664.12312>.
- Bolam, S.G., Coggan, R.C., Eggleton, J., Diesing, M., Stephens, D., 2014. Sensitivity of macrobenthic secondary production to trawling in the English sector of the Greater North Sea: a biological trait approach. *J. Sea Res.* 85, 162–177. <https://doi.org/10.1016/j.seares.2013.05.003>.
- Brown, C.J., Smith, S.J., Lawton, P., Anderson, J.T., 2011. Benthic habitat mapping: a review of progress towards improved understanding of the spatial ecology of the seafloor using acoustic techniques. *Estuar. Coast Shelf Sci.* 92, 502–520. <https://doi.org/10.1016/j.ecss.2011.02.007>.
- Collier, J.S., Brown, C.J., 2005. Correlation of sidescan backscatter with grain size distribution of surficial seabed sediments. *Mar. Geol.* 214, 431–449. <https://doi.org/10.1016/j.margeo.2004.11.011>.
- Damveld, J.H., van der Reijden, K.J., Cheng, C., Koop, L., Haaksma, L.R., Walsh, C.A.J., Soetaert, K., Borsje, B.W., Govers, L.L., Roos, P.C., Olff, H., Hulscher, S.J.M.H., 2018. Video transects reveal that tidal sand waves affect the spatial distribution of benthic organisms and sand ripples. *Geophys. Res. Lett.* 45, 837–846. <https://doi.org/10.1029/2018GL079858>.
- de Groot, S.J., 1984. The impact of bottom trawling on benthic fauna of the North Sea. *Ocean Manag.* 9, 177–190.
- De Moustier, C., Matsumoto, H., 1993. Seafloor acoustic remote sensing with multibeam and bathymetric sidescan sonar systems. *Mar. Geophys. Res.* 15, 27–42. <https://doi.org/10.1007/BF01204150>.
- Dubois, S., Retière, C., Olivier, F., 2002. Biodiversity associated with Sabellaria alveolata (Polychaeta: Sabellariidae) reefs: effects of human disturbances. *J. Mar. Biol. Assoc. U. K.* 82, 817–826. <https://doi.org/10.1017/S0025315402006185>.
- Eigaard, O.R., Bastardie, F., Hintzen, N.T., Buhl-Mortensen, L., Buhl-Mortensen, P., Catarino, R., Dinesen, G.E., Egekvist, J., Fock, H.O., Geitner, K., Gerritsen, H.D., González, M.M., Jonsson, P., Kavadas, S., Laffargue, P., Lundy, M., Gonzalez-Mirelis, G., Nielsen, J.R., Papadopoulou, N., Posen, P.E., Pulcinella, J., Russo, T., Sala, A., Silva, C., Smith, C.J., Vanelslander, B., Rijnsdorp, A.D., 2017. The footprint of bottom trawling in European waters: distribution, intensity, and seabed integrity. *ICES J. Mar. Sci.* 74, 847–865. <https://doi.org/10.1093/icesjms/fsw194>.
- Ellis, J.R., Maxwell, T., Schratzberger, M., Rogers, S.I., 2011. The benthos and fish of offshore sandbank habitats in the southern North Sea. *J. Mar. Biol. Assoc. U. K.* 91, 1319–1335. <https://doi.org/10.1017/S0025315410001062>.
- Frid, C.L.J., Harwood, K.G., Hall, S.J., Hall, J.A., 2000. Long-term changes in the benthic communities on North Sea fishing grounds. *ICES J. Mar. Sci.* 57, 1303–1309. <https://doi.org/10.1006/jmsc.2000.0900>.
- García-Charton, J.A., Pérez-Ruzafa, Á., Sánchez-Jerez, P., Bayle-Sempere, J.T., Reñones, O., Moreno, D., 2004. Multi-scale spatial heterogeneity, habitat structure, and the effect of marine reserves on Western Mediterranean rocky reef fish assemblages. *Mar. Biol.* 144, 161–182. <https://doi.org/10.1007/s00227-003-1170-0>.
- Gibb, N., Tillin, H., Pearce, B., Tyler-Walters, H., 2014. Assessing the Sensitivity of Sabellaria Spinulosa Reef Biotopes to Pressures Associated with Marine Activities. Peterborough, United Kingdom.
- Godet, L., Fournier, J., Jaffré, M., Desroy, N., 2011. Influence of stability and fragmentation of a worm-reef on benthic macrofauna. *Estuar. Coast Shelf Sci.* 92, 472–479. <https://doi.org/10.1016/j.ecss.2011.02.003>.
- Gravina, M.F., Cardone, F., Bonifazi, A., Bertrandino, M.S., Chimentì, G., Longo, C., Marzano, C.N., Moretti, M., Lisco, S., Moretti, V., Corriero, G., Giangrande, A., 2018. Sabellaria spinulosa (Polychaeta, Annelida) reefs in the Mediterranean Sea: habitat mapping, dynamics and associated fauna for conservation management. *Estuar. Coast Shelf Sci.* 200, 248–257. <https://doi.org/10.1016/j.ecss.2017.11.017>.
- Heathershaw, A.D., Codd, J.M., 1986. Depth-controlled changes in grain size and carbonate content on a shelf-edge sand bank. *Mar. Geol.* 72, 211–224. [https://doi.org/10.1016/0025-3227\(86\)90120-9](https://doi.org/10.1016/0025-3227(86)90120-9).
- Hellequin, L., Boucher, J.-M., Lurton, X., 2003. Processing of high-frequency multibeam echo sounder data for seafloor characterization. *IEEE J. Ocean. Eng.* 28, 1–11. <https://doi.org/10.1109/JOE.2002.808205>.
- Houziaux, J.-S., Fettweis, M., Francken, F., Van Lancker, V., 2011. Historic (1900) seafloor composition in the Belgian-Dutch part of the North Sea: A reconstruction based on calibrated visual sediment descriptions. *Contin. Shelf Res.* 31, 1043–1056. <https://doi.org/10.1016/j.csr.2011.03.010>.
- Houziaux, J.-S., Kerckhof, F., Degrenedele, K., Roche, M., Norro, A., 2008. The Hinder Banks: yet an important area for the Belgian marine biodiversity? Scientific Support Plan for a Sustainable Development Policy, Brussels, Belgium.
- Jackson, D.R., Briggs, K.B., 1992. High-frequency bottom backscattering: roughness versus sediment volume scattering. *J. Acoust. Soc. Am.* 92, 962–977. <https://doi.org/10.1121/1.403966>.
- Jenkins, C., Eggleton, J., Albrecht, J., Barry, J., Duncan, G., Golding, N., O'Connor, J., 2015. North Norfolk Sandbank and Saturn Reef cSAC/SCI Management Investigation Report.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373–386. <https://doi.org/10.2307/3545850>.
- Jones, J.B., 1992. Environmental impact of trawling on the seabed: a review. *N. Z. J. Mar. Freshw. Res.* 26, 59–67. <https://doi.org/10.1080/00288330.1992.9516500>.
- Knaapen, M.A.F., 2009. Sandbank occurrence on the Dutch continental shelf in the North Sea. *Geo Mar. Lett.* 29, 17–24. <https://doi.org/10.1007/s00367-008-0105-7>.
- Knaapen, M.A.F., 2005. Sandwave migration predictor based on shape information. *J. Geophys. Res.* Earth Surf. 110, F04S11. <https://doi.org/10.1029/2004JF000195>.
- Koch, E.W., Ackerman, J.D., Verduin, J., van Keulen, M., 2006. Fluid dynamics in seagrass ecology - from molecules to ecosystems. In: Larkum, A.W.D., Orth, R.J., Duarte, C. (Eds.), *Seagrasses: Biology, Ecology and Conservation*. Springer, Dordrecht, the Netherlands, pp. 193–225.
- Koop, L., Amiri-Simkooei, A., van der Reijden, K.J., O'Flynn, S., Snellen, M., Simons, D.G., 2019. Seafloor classification in a sand wave environment on the Dutch continental shelf using multibeam echosounder backscatter data. *Geosciences* 9, 142. <https://doi.org/10.3390/geosciences9030142>.
- Lovett, G.M., Jones, C.G., Turner, M.G., Weathers, K.C., 2006. Ecosystem Function in Heterogeneous Landscapes, Ecosystem Function in Heterogeneous Landscapes. Springer, New York, United States. https://doi.org/10.1007/0-387-24091-8_1.
- MacArthur, R.H., Wilson, E.O., 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton.
- Mazières, A., Gillet, H., Idier, D., Mulder, T., Garland, T., Mallet, C., Marieu, V., Hanquiez, V., 2015. Dynamics of inner-shelf, multi-scale bedforms off the south Aquitaine coast over three decades (Southeast Bay of Biscay, France). *Contin. Shelf Res.* 92, 23–36. <https://doi.org/10.1016/j.csr.2014.11.002>.
- McConnaughey, R.A., Mier, K.L., Dew, C.B., 2000. An examination of chronic trawling effects on soft-bottom benthos of the eastern Bering Sea. *ICES J. Mar. Sci.* 57, 1377–1388. <https://doi.org/10.1006/jmsc.2000.0906>.

- Nieuwenhuize, J., Maas, Y.E.M., Middelburg, J.J., 1994. Rapid analysis of organic carbon and nitrogen in particulate materials. *Mar. Chem.* 45, 217–224. [https://doi.org/10.1016/0304-4203\(94\)90005-1](https://doi.org/10.1016/0304-4203(94)90005-1).
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2017. *vegan: Community Ecology Package*. R package version 2.4-4. <https://CRAN.R-project.org/package=vegan>.
- Passchier, S., Kleinhans, M.G., 2005. Observations of sand waves, megaripples, and hummocks in the Dutch coastal area and their relation to currents and combined flow conditions. *J. Geophys. Res.* 110, F04S15 <https://doi.org/10.1029/2004JF000215>.
- Pearce, B., 2014. *The Ecology of Sabellaria Spinulosa Reefs*. Plymouth University.
- Queirós, A.M., Birchenough, S.N.R., Bremner, J., Godbold, J.A., Parker, R.E., Romero-Ramirez, A., Reiss, H., Solan, M., Somerfield, P.J., Van Colen, C., Van Hoey, G., Widdicombe, S., 2013. A bioturbation classification of European marine infaunal invertebrates. *Ecol. Evol.* 3, 3958–3985. <https://doi.org/10.1002/ece3.769>.
- R Core Team, 2018. R: a language and environment for statistical computing. R Found. Stat. Comput., R Foundation for Statistical Computing. <https://doi.org/10.1007/978-3-540-74686-7>.
- Rabaut, M., Guilini, K., Van Hoey, G., Vincx, M., Degraer, S., 2007. A bio-engineered soft-bottom environment: the impact of *Lanice conchilega* on the benthic species-specific densities and community structure. *Estuar. Coast Shelf Sci.* 75, 525–536. <https://doi.org/10.1016/j.ecss.2007.05.041>.
- Ramey, P.A., Grassle, J.P., Grassle, J.F., Petrecca, R.F., 2009. Small-scale, patchy distributions of infauna in hydrodynamically mobile continental shelf sands: do ripple crests and troughs support different communities? *Contin. Shelf Res.* 29, 2222–2233. <https://doi.org/10.1016/j.csr.2009.08.020>.
- Rhoads, D.C., Cande, S., 1971. Sediment profile camera for in situ study of organism-sediment relations. *Limnol. Oceanogr.* 16, 110–114. <https://doi.org/10.4319/lo.1971.16.1.0110>.
- Rijnsdorp, A.D., Bolam, S.G., Garcia, C., Hiddink, J.G., Hintzen, N.T., van Denderen, P. D., van Kooten, T., 2018. Estimating sensitivity of seabed habitats to disturbance by bottom trawling based on the longevity of benthic fauna. *Ecol. Appl.* 28, 1302–1312. <https://doi.org/10.1002/eap.1731>.
- Sciberras, M., Hiddink, J.G., Jennings, S., Szostek, C.L., Hughes, K.M., Kneafsey, B., Clarke, L.J., Ellis, N., Rijnsdorp, A.D., McConnaughey, R.A., Hilborn, R., Collie, J.S., Pitcher, C.R., Amoroso, R.O., Parma, A.M., Suuronen, P., Kaiser, M.J., 2018. Response of benthic fauna to experimental bottom fishing: a global meta-analysis. *Fish. Fish.* 19, 698–715. <https://doi.org/10.1111/faf.12283>.
- Simons, D.G., Snellen, M., 2009. A Bayesian approach to seafloor classification using multi-beam echo-sounder backscatter data. *Appl. Acoust.* 70, 1258–1268. <https://doi.org/10.1016/j.apacoust.2008.07.013>.
- Snelgrove, P.V.R., 1994. Getting to the bottom of marine biodiversity: sedimentary habitats. *Bioscience* 49, 129–138. <https://doi.org/10.2307/1313538>.
- Solan, M., Cardinale, B.J., Downing, A.L., Engelhardt, K.A.M., Ruesink, J.L., Srivastava, D.S., 2004. Extinction and ecosystem function in the marine benthos. *Science* 306, 1177–1180. <https://doi.org/10.1126/science.1103960> (80-).
- Temmerman, S., Bouma, T.J., Govers, G., Wang, Z.B., De Vries, M.B., Herman, P.M.J., 2005. Impact of vegetation on flow routing and sedimentation patterns: three-dimensional modeling for a tidal marsh. *J. Geophys. Res. Earth Surf.* 110, 1–18. <https://doi.org/10.1029/2005JF000301>.
- Thrush, S.F., Dayton, P.K., 2002. Disturbance to marine benthic habitats by trawling and dredging: implications for marine biodiversity. *Annu. Rev. Ecol. Systemat.* 33, 449–473. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150515>.
- Tilman, D., 1982. *Resource Competition and Community Structure*. Princeton University Press, Princeton.
- Trentesaux, A., Stolk, A., Tessier, B., Chamley, G., 1994. Surficial sedimentology of the middelkerke bank (southern North sea). *Mar. Geol.* 121, 43–55. [https://doi.org/10.1016/0025-3227\(94\)90155-4](https://doi.org/10.1016/0025-3227(94)90155-4).
- van der Reijden, K.J., Hintzen, N.T., Govers, L.L., Rijnsdorp, A.D., Olf, H., 2018. North Sea demersal fisheries prefer specific benthic habitats. *PLoS One* 13, e0208338. <https://doi.org/10.1371/journal.pone.0208338>.
- van der Reijden, K.J., Koop, L., O'Flynn, S., Garcia, S., Bos, O., van Sluis, C., Maaholm, D. J., Herman, P.M.J., Simons, D.G., Olf, H., Ysebaert, T., Snellen, M., Govers, L.L., Rijnsdorp, A.D., Aguilar, R., 2019. Discovery of *Sabellaria spinulosa* reefs in an intensively fished area of the Dutch continental shelf, North Sea. *J. Sea Res.* 144, 85–94. <https://doi.org/10.1016/j.seares.2018.11.008>.
- van der Zee, E.M., van der Heide, T., Donadi, S., Eklöf, J.S., Eriksson, B.K., Olf, H., van der Veer, H.W., Piersma, T., 2012. Spatially extended habitat modification by intertidal reef-building bivalves has implications for consumer-resource interactions. *Ecosystems* 15, 664–673. <https://doi.org/10.1007/s10021-012-9538-y>.
- van Dijk, T.A.G.P., van Dalen, J.A., Van Lancker, V., van Overmeeren, R.A., van Heteren, S., Doornbal, P.J., 2012. Benthic habitat variations over tidal ridges, North Sea, The Netherlands. In: Harris, P., Baker, E. (Eds.), *Seafloor Geomorphology as Benthic Habitat*. Elsevier Inc., London, United Kingdom, pp. 241–249. <https://doi.org/10.1016/B978-0-12-385140-6.00013-X>.
- Van Lancker, V., Moerkerke, G., Du Four, I., Verfaillie, E., Rabaut, M., Degraer, S., 2012. Fine-scale geomorphological mapping of sandbank environments for the prediction of macrobenthic occurrences, Belgian Part of the North Sea. In: Harris, P., Baker, E. (Eds.), *Seafloor Geomorphology as Benthic Habitat*. Elsevier Inc., London, United Kingdom, pp. 251–260. <https://doi.org/10.1016/B978-0-12-385140-6.00014-1>.
- Wallis, B., Salvador de Paiva, J., van Prooijen, B.C., Ysebaert, T., Smaal, A.C., 2015. The ecosystem engineer *Crassostrea gigas* affects tidal flat morphology beyond the boundary of their reef structures. *Estuar. Coast* 38, 941–950. <https://doi.org/10.1007/s12237-014-9860-z>.
- Zeiler, M., Schwarzer, K., Ricklefs, K., 2008. Seabed morphology and sediment dynamics. *Die Küste* 74, 31–44.