



Sediment migrations drive the dynamic of macrobenthic ecosystems in subtidal sandy bedforms



Alexandre Elie Robert ^{a,b,*}, Nolwenn Quillien ^a, Mahmoud Bacha ^c, Clémence Caulle ^d, Maëlle Nexer ^a, Briz Parent ^d, Thierry Garlan ^e, Nicolas Desroy ^b

^a France Energies Marines Environmental Integration R&D Program, 525 Avenue Alexis de Rochon, 29280 Plouzané, France

^b IFREMER, Unité Littoral, Laboratoire Environnement et Ressources de Bretagne Nord, CRESCO, 38 rue du Port-Blanc, Dinard 35800, France

^c Laboratoire d'Océanologie et de Géosciences, UMR 8187, CNRS, Université du Littoral Côte d'Opale, 32 Avenue Foch, 62930 Wimereux, France

^d Ocean Zoom, 2 chemin de la Houssinière, 44300 Nantes, France

^e Shom, 29200 Brest, France

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ABSTRACT

A traditional taxonomic approach coupled to a biological traits analysis was conducted in order to provide a new insight into macrobenthic communities associated with subtidal sandy environments. Results suggest that the macro-scale distribution of benthic communities is mainly driven by the migration rate of bedforms (sandbank, barchan dune and transversal dune) which changes the sediment grain size and reduces macrobenthic diversity. A classic scheme of species/traits succession was also observed from less to more physically disturbed areas. Finally, the high frequency of migration events homogenized macrobenthic communities between the troughs to the crest of bedforms. As bedforms areas are targeted for the commissioning of offshore windfarms the information provided by the present paper will be particularly useful to implement the environmental impact assessment required for such activities at sea.

1. Introduction

Subtidal sandy bedforms are largely represented worldwide, in macrotidal areas. On the French continental shelf, they are numerous in the Dover straight, the western English Channel, and the Iroise and Celtic Seas. Bedforms can be classified in three principal structures depending on their morphology: sandbank, dunes and ripples (see the classification of subaqueous bedforms by [Ashley, 1990](#)). Sandbank are oriented parallel to the main current direction and can be ten kilometers length for ten meters high. Dunes are perpendicular to the current ([Aernouts, 2005](#); [De Moor, 2002](#); [Haerens et al., 2012](#); [Le Bot et al., 2005](#); [Van Cauwenbergh, 1971](#); [Van Lancker et al., 2009](#)) and generally display a couple of meters high (although “megadunes” with a 2 to 7 m height and a wave lengths of 150–500 m have been observed; [Haerens et al., 2012](#)). Sand ripples are small bed forms, less than 1-m height, grouped in large fields. These structures also differ in their dynamics: sandbanks are stable over hundreds of years whereas subtidal dunes are known to be mobile, moving up to one hundred meters per year in the southern bight of the North Sea ([Le Bot, 2001](#)). The morphology of sand ripples changes at short time scale (tidal cycle). Differences in migration

speeds depend on several factors such as storm and tidal currents, depth, grain size and dune size ([Ernstsen et al., 2004](#); [Ferret, 2011](#); [Garlan, 2004](#); [Le Bot, 2001](#)). Inter-annual to decennial variability in storm activity may also be strongly influential ([Ferret et al., 2010](#)).

Bedforms, constitute important habitats where 30% of the species are endemic (J. Grall, com. pers.) and are under the particular protection of the NATURA 2000 directive. In the Flanders bank, this protection status is also justified by the presence of marine mammals of Community interest. Knowledge on benthic communities inhabiting sandy bedforms stems from large-scale studies that did not specifically target these habitats (e.g. [Desroy, 2002](#): 800 km²; [Van Hoey et al., 2004](#): 2600 km²). They revealed the presence of two principal macrobenthic communities distributed according to the seabed substrate. Beyond the influence of the sediment cover, a coast-offshore gradient can be superimposed, under certain conditions such as the influence of a coastal river linked to the fresh water inflows from the Seine and the Somme rivers. The first assemblage is found on a medium to fine sand and is widely distributed within bedforms. It is mainly typified by the polychaetes *Nephtys cirrosa* and *Ophelia borealis*. In the French part of the North Sea, [Desroy \(2002\)](#) found a remarkably low diversity and density in this assemblage with

* Corresponding author at: France Energies Marines Environmental Integration R&D Program, 525 Avenue Alexis de Rochon, 29280 Plouzané, France.
E-mail address: alexandre.robert@ifremer.fr (A.E. Robert).

4.7 species. 0.5 m^{-2} and 19.2 ind. 0.5 m^{-2} . In the Belgian parts of the North Sea, Breine et al. (2018) also reported low diversities and densities ($9.1 \pm 4.1\text{ species}\cdot\text{m}^{-2}$ and $367.8 \pm 359.9\text{ ind}\cdot\text{m}^{-2}$). The second assemblage is patchier and located in depressions separating sandbanks. It is typified by muddy heterogeneous sediments and by the presence of *Magelona johnstoni* and *Hesionura elongate*. Both studies revealed higher values of species richness and density than in medium to fine sands. Indeed, Desroy (2002) recorded 11.7 species. 0.5 m^{-2} and 113.4 ind. 0.5 m^{-2} whereas Breine et al. (2018) found $14.0 \pm 5.4\text{ species}\cdot\text{m}^{-2}$ and $724.0 \pm 746.1\text{ ind}\cdot\text{m}^{-2}$. At smaller spatial scales, a few studies have revealed a decrease in species richness, abundance and Shannon's diversity index along the slope of bedforms, from the trough to the crest, in relation to grain size increase (Baptist et al., 2006; Damveld et al., 2018; Ellis et al., 2011; Ferret, 2011; Mestdagh et al., 2020; van Dijk et al., 2012).

Above-mentioned studies were based on taxonomic approaches and, *de facto*, did not consider the role played by the species in this ecosystem. Hence, the benthic ecosystem functioning of sandy bedforms still remains poorly known. To our knowledge, only Breine et al. (2018) addressed this issue at large scale but they did not investigate how the ecosystem functioning vary between the trough and the crest of bedforms and across bedform types. As the existence/maintenance of biological functions is considered a key factor in sustaining goods and services provided by ecosystems, it becomes increasingly important to consider not only structural features of benthic communities, but also their functional attributes (Lavorel, 2013; Pinto et al., 2014; Worm et al., 2006). For this purpose, Biological Traits Analyses (BTA) are becoming extremely popular because traits (*i.e.* life history, morphological and behavioral characteristics of a species) are considered proxy of the intensity of ecosystem processes (Bremner et al., 2006a; Bremner, 2008). BTA have also been successfully used to investigate how benthic communities respond to physical disruptions such as dredging deposition (Bolam, 2012), marine aggregate extraction (Cooper et al., 2008; Froján et al., 2011; Wan Hussin et al., 2012), bottom-trawling (de Juan et al., 2007; van Denderen et al., 2015; Tillin et al., 2006) and metal contamination (Piló et al., 2016).

Bedforms areas are currently targeted by Offshore Renewable Energy (ORE) industries because of the high hydrodynamicism as well as strong and constant wind regimes that typify such environments (Miall, 2013). Sands are also relatively easy to work, for instance for the burying of export cables (Taormina et al., 2018). It is thus urgent to provide a deeper understanding on the dynamic of benthic ecosystem functioning in order to anticipate the potential impacts of the ORE industry on bedforms habitats.

The present study aims to improve the knowledge on the spatio-temporal dynamic of benthic communities associated with bedforms. It focuses on the French Flander bank, where the implementation of a wind farm is under consideration. Two hypotheses are tested in this study, thanks to the combination of taxonomic and BTA approaches:

H1. Benthic communities differ spatially (across bedforms) and temporally (between seasons), in relation with natural sources of disruption such as bedform migrations.

H2. Benthic communities differ within a given type of bedform (from the trough to the crest), in relation with the distribution of sediment grain size.

2. Material & methods

2.1. Sampling strategy

The present study focused on an 80 km^2 area located within the French Flander bank, offshore the Dunkirk harbor (Fig. 1; see the description in Desroy, 2002 and Davoult et al., 1988). The study area was chosen because it exhibits a large variety of bedforms and is targeted for the future commissioning of an offshore wind farm. In this area, sandy sediments are arranged into large sandbanks covered by dunes which themselves bear ripples. It is, however, possible to identify several "individual" bedforms.

The spatio-temporal dynamic of macrobenthic communities was assessed using a stratified sampling design (Figs. 1 and 2), defined from a previous bathymetric survey conducted between 2016 and 2017 by the

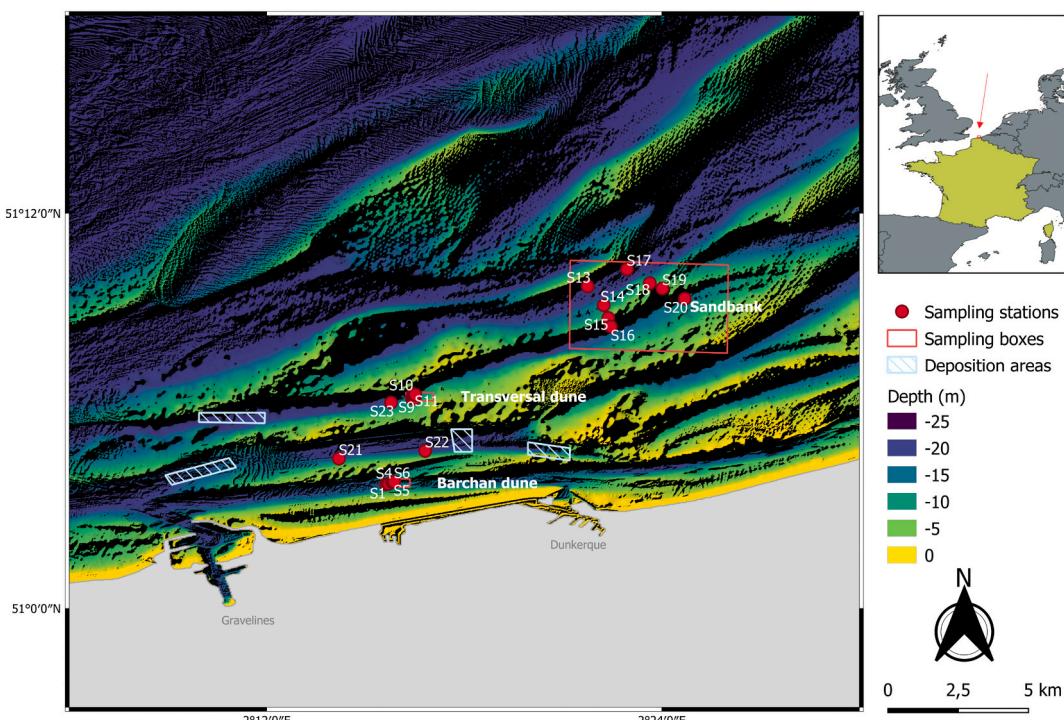


Fig. 1. Map of the sampling strategy superimposed on the digital terrain model provided by the French Navy's Hydrographic and Oceanographic department at a 0.0002° resolution (around 20 m) (SHOM, 2016). Details on the transversal dune and on the barchan dune are represented on Fig. 2.

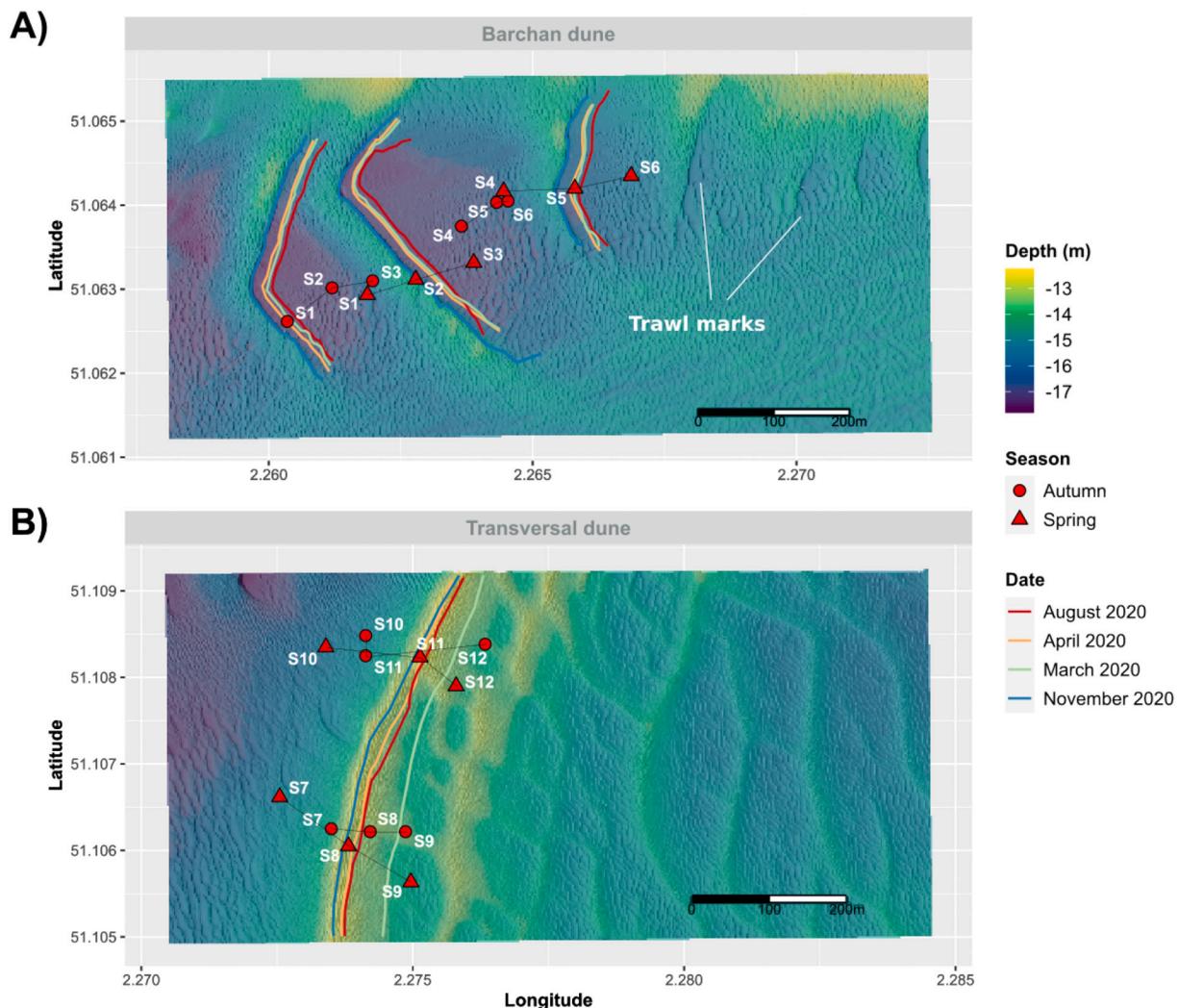


Fig. 2. Evolution of the position of the crests on A) the barchan dunes and B) on the transversal dune. Crest lines are superimposed on the bathymetric chart obtained in November 2019. The position of each sampling station is also indicated. The height of the barchan dunes and of the transversal dune was 3 and 4 m, respectively. Their wavelength was around 50 m.

French Navy's Hydrographic and Oceanographic Department (SHOM). In the area investigated, three morphological bedform types were identified inside sampling areas called "boxes" (Fig. 1):

- Box 1 is located 2 km offshore, at a depth ranging between -10 and -15 m. It includes three barchan dunes (*i.e.* dunes with a crescent-shape; Fig. 2);
- Box 2 is located 6 km offshore, at a depth ranging between -4 and -12 m, in an area where transversal dunes occur (*i.e.* dunes which are straight-lined; Fig. 2);
- Box 3 is located 10 km offshore, at a depth ranging from -6 to -19 m. It is typified by a sandbank called "Binnen Ratel" (*i.e.* large bedforms which are oriented parallel to the main current direction; Fig. 1).

Several bathymetric surveys were performed in 2019 and 2020 in boxes 1 and 2 in order to investigate how dunes migrate both in space and time. No bathymetric survey was performed within box 3, as sandbanks are considered stable over hundreds of years (see Aernouts, 2005; De Moor, 2002; Van Cauwenbergh, 1971).

Sampling of sediment and macrofauna was performed in the autumn of 2019 (October) and the spring of 2020 (May) at 23 stations. The objective was to sample four stations from the trough to the crest of

transversal and barchan dunes and to sample six stations from the trough to the crest of sandbanks. Three additional stations (S21, S22 and S23) were positioned within a reference area, free from bedforms.

In the field, the vessel depth-sounder was used to precisely position sampling stations on bedforms. Despite this, the relatively small size of the bedforms and the strength of the tidal currents make the *in situ* positioning of the station very difficult. Such difficulties are however inherent to this kind of small-scale study and similar difficulties have also been reported by Ferret (2011) and Mestdagh et al. (2020). As a consequence, all stations sampled within barchan dunes were located in their troughs with the exception of stations S2 and S5 which were located on crests during the spring survey (Fig. 2A). The distribution of stations was better-balanced on the transversal dune (Fig. 2B), with respectively two stations located on the crests (S8 and S11), on the slope (S9 and S12) and in the trough (S7 and S10; except during autumn when the station S7 was located on the slope). The sandbank, which is a relatively large bedform compared to barchan and transversal dunes, was more easily sampled. Indeed, two stations (S15 and S19) were positioned on the top of the bank and four stations were located on the slope (S14, S16, S18 and S20). Only one station (S13) was sampled in the depression that separated two sandbanks. The presence of gravel on the seabed prevented the sampling of the second station (S17) with the Van Veen grab. Finally, within the reference area, depth was of -17.2 ± 1.1

m with no clear variation, as planned.

Three replicates were collected at each sampling station using a Van Veen grab (0.1 m^2), approximately with a 5–10 m accuracy in the positioning (the vessel size was 20 m length overall). Samples were gently washed *in situ* through a 1 mm sieve and preserved in 4.5% formalin before being sorted, identified and counted in the laboratory. The proportion of juveniles relative to the adults has been estimated for each species during the identification process for subsequent use as biological trait (see Section 2.2).

One additional replicate was sampled per station for the study of sedimentary characteristics. Grain-size analyses were performed using a standardized AFNOR set of 17 sieves, as recommended by the protocols established for the Water Framework Directive (Garcia et al., 2014). The sediment retained on each sieve was weighted with a 1 mg-accuracy. Then, the median grain size, a geometric sorting index (which increases as the sorting of the sediment decreases; Folk and Ward, 1957) as well as the mud proportion ($<63 \mu\text{m}$) were calculated using the Rysgran package (Gilbert et al., 2012) under R statistical software (R Core Team, 2013).

2.2. Structural and functional diversity of macrobenthic communities

The structural diversity of benthic communities was assessed by calculating several indicators summarizing the number and distribution of species at each station: the species richness (S), total abundance, total biomass as well as Pielou's evenness (J').

Functional diversity of benthic communities was studied using a Biological Trait Analysis (BTA) (Bremner et al., 2003). A total of 9 traits were selected, which is above the optimum number of 8 traits needed for sound functional analyses, as identified by Laughlin (2014) based on a review of the literature. Selected traits were the mobility, fragility, position on substrata, average size, feeding mode, life span, egg development, larval development and life stage (Table 1). By choosing traits also used by de Juan and Demestre (2012) to design a Trawling Disturbance Index (TDI), we assumed that natural and anthropogenic sources of disruptions are likely to alter macrobenthic communities in a similar manner, as shown by van Denderen et al. (2015). Moreover, traits relative to the reproduction and to the development inform on dispersal capacity of macrobenthic populations and communities as well as on their dynamics in sublittoral sediments (Pacheco et al., 2013).

Then, the 9 traits were split in 31 modalities. A score was attributed to each species in order to reflect their affinity to each modality, following the fuzzy-coding principle (Chevène et al., 1994): a score of 0 means no affinity whereas a score of 3 stands for full affinity of a species to a given modality. For the trait life stage, the score corresponded to the ratio between the abundance of juvenile and the abundance of adult in the community. The other scores were attributed from data available on the online BIOTIC database (MarLIN, 2006) or completed thanks to published (Foveau et al., 2020) or unpublished databases (Garcia unpublished data; Sturbois et al., unpublished data; Rigolet et al., unpublished data). In case of missing data for certain species, scores of the higher taxonomic level (mostly genus level) were attributed. When it was impossible to get information for a species (e.g. feeding mode of nematodes), a value of 0 was attributed in each modality. It is thus implicitly replaced by the average profile for the corresponding trait. As a consequence, a species with such a score is not taken into account in the calculation of the column weight (Chevène et al., 1994). Biological traits scores used for the present study have been published as open access database in the SEANOE portal (Robert et al., 2021; doi:10.17882/80785). Once the fuzzy-coding matrix established, score proportions were scaled between 0 and 1 and combined with the species biomass (canonical scalar product) to obtain a Community-level Weighted Means (CWM) matrix of trait values (Bremner, 2008; Bremner et al., 2006a, 2006b).

Four univariate indices of functional diversity were calculated based on the position of species within a multidimensional space of traits

Table 1

Definition of the biological traits and modalities used in the present study and adapted from Breine et al. (2018) and de Juan and Demestre (2012).

Traits	Modalities	Definition
Mobility	Sessile Highly mobile (swimming) Mobile (crawl/creep/climb) Sedentary	Species which have no mobility Species that actively swim in the water column (many usually return to the seabed when not feeding) Capable of some movement along the sediment surface or rocky substrata Species in which adults are capable of active, but limited, movement within the sediment (e.g. burrowers, tubicolous organisms)
Fragility	Robust Strong No protection Fragile shell/structure	Hard shell Species flexible and/or with regeneration ability Species have no structure able to protect them against physical disruptions (natural or anthropogenic) Species have fragile structures (e.g. thin shell) which are unable to protect them against physical disruptions (natural or anthropogenic)
Position on substrata	Emergent Surface Sub-surface burrowing (first cm) Deep burrowing	Species living above the seabed Species living at the sediment-water interface Species found between 0 and 5 cm below the sediment surface Species found below the sediment surface at a depth greater than 5 cm
Average size	Small Medium Large	Length or height of the adults below 2 cm Length or height of the adults between 2 and 10 cm Length or height of the adults >10 cm
Feeding mode	Suspension feeders Deposit feeders Predator/Scavenger	The removal of particulate food from the water column, generally via filter-feeding Active removal of detrital material from the sediment surface or from within the sediment matrix. This class includes species which scrape and/or graze algal matter from surface Species which feed upon living or dead animals
Egg development	Asexual/Budding Sexual shed eggs-pelagic Sexual shed eggs-benthic Sexual brood eggs	Species can reproduce asexually, either by fragmentation, budding, epitoky. Often this is in addition to some form of sexual reproduction Eggs/spawns are released into the water column Eggs are released into/onto the seabed, either free or maintained on seabed by mucous or other means Eggs are maintained by adult for protection, either within parental tube or within body cavity
Larval development	Planktotrophic Lecitotrophic Direct	Larvae feed and grow in the water column Larvae feed on yolk reserves Larval stage missing (eggs develop into juvenile forms) or larvae are limited to the seabed
Life span	I < 1 II-2(>1,<3) III-10 I > 10	The maximum life span of the adult stage in years (y)

(Principal COordinate Analysis: see the review of Mouillot et al., 2013) and by considering fuzzy traits as continuous variables. The functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv), as primary components of functional diversity (Mason et al., 2005), were calculated following the method of Villéger et al. (2008). The functional redundancy (FRed) was also calculated as the ratio of Functional Diversity to Shannon–Weaver index (FD/H') (van der Linden

et al., 2012). FRed values decrease as the functional redundancy increases. Functional diversity indicators were calculated using the "FD" package (Laliberté et al., 2014).

2.3. Data analysis

A permutational multivariate analysis of variance (PERMANOVA; Anderson, 2005, 2001), was used to test how the sedimentary characteristics (grain size per station), the structural diversity (with log+1 transformed biomass of species as cell values) and the functional diversity (CWM weighted by the log+1 transformed biomass) were distributed between (i) the type of bedform, (ii) the season and (iii) the depth as proxy of the position on a bedform. Then, the effects of each parameter were characterized according to their rank in the PERMANOVA, using either pairwise-Wilcoxon tests (bedforms and the season) or linear regressions (depth) for univariate descriptors. Principal component analysis (PCA), non-metric multidimensional scaling (nMDS; Bray-Curtis distance, 1000 random permutations) and fuzzy-principal component analysis (FPCA) were used to describe the multivariate variations in sedimentary characteristics as well as structural and functional diversities. The nMDS was associated with a Simper test (Clarke, 1993) in order to determine which species were responsible for the spatio-temporal variations in the benthic community structure.

Multiple linear regression models were used to link the univariate indicators of structural and functional diversity with the sedimentary characteristics. Multivariate relationships between the macrobenthic community structure and the sedimentary characteristics, as well as relationships between the CWM and the sedimentary characteristics, were assessed using a distance-based redundancy analysis (dbRDA) with the Bray-Curtis and the Gower distances as measures of the dissimilarity. A stepwise procedure based on the Akaike Information Criterion (AIC) was followed in order to only add relevant variables in the models.

3. Results

3.1. Bedform morpho-dynamic

Barchan dunes were N-S oriented (Fig. 2A). They were 3 m high (with a depth ranging between 17.5 and 14.5 m) and their wavelength was approximately 50 m. Migration of barchan dunes looked oscillatory: after having migrated by 22 ± 10 m eastward between November 2019 and March 2020 as attested by the orientation of their steep slope, they backed up by 6 ± 4 m westward between March and April 2020. Barchan dunes finally moved by 12 ± 4 m eastward between April and August 2020, which corresponded to a total displacement of 40 m.

The transversal dune was also N-S oriented and its height and width were relatively similar as those of the barchan dunes: 4 m height for depth ranging between 9 and 5 m and a 50 m wavelength (Fig. 2B). The migration of the transversal dune was similar to that of the barchan dunes in terms of direction, but with longer displacements. Migration was of 56 ± 10 m eastward between November 2019 and March 2020, of 45 ± 8 m westward between March and April 2020 and of 7 ± 3 m eastward between April and August 2020. Over the ten-month period, the transversal dune displayed a cumulative displacement of around 108 m.

Conversely to the other bedforms, the sandbank was parallel to the coast (SW-NE oriented, Fig. 1). It was 21 m high (with a depth ranging between 25 and 4 m) for a 2.5 km width. Remember that sandbank migration has not been assessed during the present study because this kind of bedform is considered stable over centuries.

3.2. Sedimentary characteristics

Sedimentary characteristics were very homogeneous over the studied area and most of the variations in the distribution of sedimentary characteristics occurred across the various bedform types (Permanova,

$R^2 = 0.35$; p -value <0.001; see supplementary information S1). As shown by the PCA (Fig. 3), sedimentary characteristics of the barchan and transversal dunes were significantly different from those of the sandbank and reference area (Table 2). Indeed, sediments of the transversal and barchan dunes showed a higher median grain size (median grain size equivalent to 397 ± 144 and 327 ± 35 μm) and were less sorted (sorting index equivalent to 1.7 ± 0.55 and 1.72 ± 0.68) than sediments of the sandbank (269 ± 32 μm and 1.51 ± 0.41) and reference area (246.75 ± 40.5 μm and 1.24 ± 0.03). The mud content was remarkably low whatever the bedform but displayed higher values within the barchan dune ($1.1 \pm 0.9\%$) and the reference area ($1.3 \pm 1.4\%$) compared to the transversal dune ($0.1 \pm 0.1\%$) and the sandbank ($0.4 \pm 1.0\%$).

Season and depth alone explained only a small part of the variance ($R^2 = 0.01$) and were not significant in the model (p -value >0.05). However, the Permanova revealed a significant interaction between the type of bedform and the depth of the sampling stations ($R^2 = 0.31$; p -value = 0.05).

Multiple linear regression models showed, for a transversal dune, a significant increase in the median grain size ($R^2 = 0.51$; p -value <0.01) and of the sorting index ($R^2 = 0.58$; p -value <0.01), as the depth decreased (Fig. 4). The median grain size was around 200 μm in the trough versus 500 μm at the crest and the sorting index increased from 1 to almost 2.5 from the trough to the crest. On barchan dunes and in the reference area, a negative but insignificant relationship existed between the median grain size and the depth: from the base of the dune to the summit for both structures, median grain size varied from 300 to 350 μm and from 250 to 300 μm , respectively. The median grain size decreased from 300 μm to 250 μm between the trough and the crest of the sandbank and the sorting index varied from around 1.8 to 1.4, but these trends were insignificant in the models.

3.3. Macrofauna communities

3.3.1. General characteristics

A total of 107 taxa was recorded during the two surveys (65 taxa in autumn 2019 and 81 in spring 2020) and 95% of the organisms were identified at species level (except nematods and nemerteans). The mean species richness (S) was of 14 ± 6 species· m^{-2} , and ranged from 5 to 35 species· m^{-2} . Abundance and biomass were of 1338 ± 4919 ind· m^{-2} and of 2921 ± 4003 mg AFDW· m^{-2} and the mean value of Pielou's evenness was of 0.6 ± 0.1 .

Overall, 15 and 18 species contributed to 95% of the total abundance and biomass, respectively. They were mainly annelids (78% of the abundance and 33% of the biomass) such as *Lanice conchilega* (only juveniles), *Spiophanes bombyx*, *Magelona filiformis*, *Hesionura elongata* and *Nephtys cirrosa* with contributions to the total abundance of 27%, 14%, 14%, 8%, 7%, respectively (Table 3). On its own, *Nephtys cirrosa* contributed to 15% of the total biomass. Arthropods contributed to 16% of the abundance and 9% of the biomass. They were mostly represented by *Bathyporeia pelagica*, *Gastrosaccus spinifer* and *Urothoe brevicornis* (8%, 3% and 1% of the total abundance). Although they represented less than 1% of the total abundance, echinoderms were mainly represented by large individuals of *Echinocardium cordatum* (recorded in 23% of sampled stations), which contributed to 46% of the total macrofauna biomass. Chordate (only represented by *Branchiostoma lanceolatum*), Cnidarian, Mollusc and Sipunculid were present but rare (less than 1% of the abundance and biomass each).

From a functional point of view, most individuals (58%) were sedentary deposit feeders with pelagic eggs and larvae. To a less extent, they were mobile predator-scavengers (25%) or small deposit feeders with a direct development or breeding eggs (17%). Most of the organisms collected were adult (94%) and juveniles only occurred in spring. Juveniles mostly belonged to 12 species: *Corytes cassivelaunus* (100% of the collected specimen), *Crangon crangon* (73%), *Diogenes pugilator* (38%), *Diplodonta rotundata* (100%), *Glycera* sp. (50%), *Lanice conchilega*

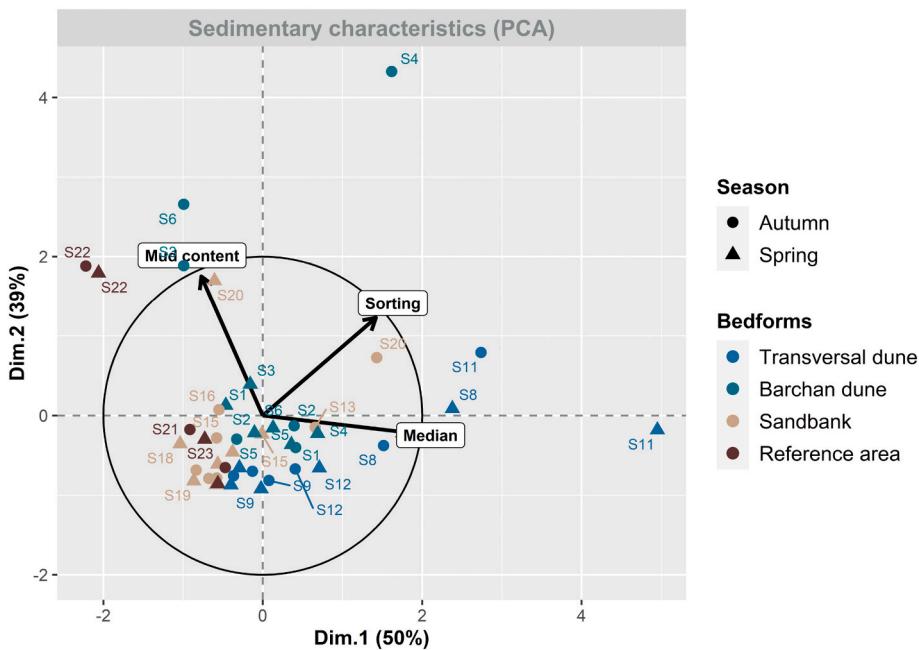


Fig. 3. PCA showing how the sedimentary characteristics were distributed between the type of bedforms, the seasons as well as the sampling stations. The superimposed circle illustrates the vectors of the variables relative to two first PCA axes. The vector length reflects the importance of that variable's contribution to the two PCA axes.

Table 2

Distribution of the sedimentary characteristics between the different bedforms and within the reference area. Letters denote significant pairwise Wilcoxon tests.

Sedimentary characteristics	Transversal dune ^a	Barchan dune ^b	Sandbank ^c	Reference area ^d
Median (μm)	$397 \pm 144^{\text{c,d}}$	$327 \pm 35^{\text{c}}$ ^d	269 ± 32	$247 \pm 40^{\text{a,b}}$
Sorting index	$1.7 \pm 0.55^{\text{d}}$	$1.72 \pm 0.68^{\text{d}}$	1.51 ± 0.41	$1.24 \pm 0.03^{\text{a,b}}$
Mud content (%)	$0.1 \pm 0.1^{\text{b,d}}$	$1.1 \pm 0.9^{\text{c}}$	$0.4 \pm 1.0^{\text{d}}$	$1.3 \pm 1.4^{\text{a,c}}$

(100%), *Liocarcinus* sp. (96%), *Macomangulus tenuis* (3%), *Mytilus edulis* (100%), *Paragnathia formica* (100%), *Pecten maximus* (100%) and *Spisula solidia* (23%).

The Permanova performed on the matrix of biomass (log+1 transformed) showed that the type of bedform (see supplementary information S1, $R^2 = 0.25$, p -value <0.001) and, to a lesser extent, seasons ($R^2 = 0.06$, p -value <0.001), were responsible for most of the variations in the macrobenthic community structure. Depth of sampling stations was conversely a poor predictor of the distribution of the macrobenthic communities (p -value >0.05). Bedform type and season ($R^2 = 0.08$, p -value <0.01) as well as bedform type and depth ($R^2 = 0.08$, p -value <0.010) significantly interacted in the model. Similar variations were observed for the traits composition (see supplementary information S1), although the season did not appear to be significant in the model (p -

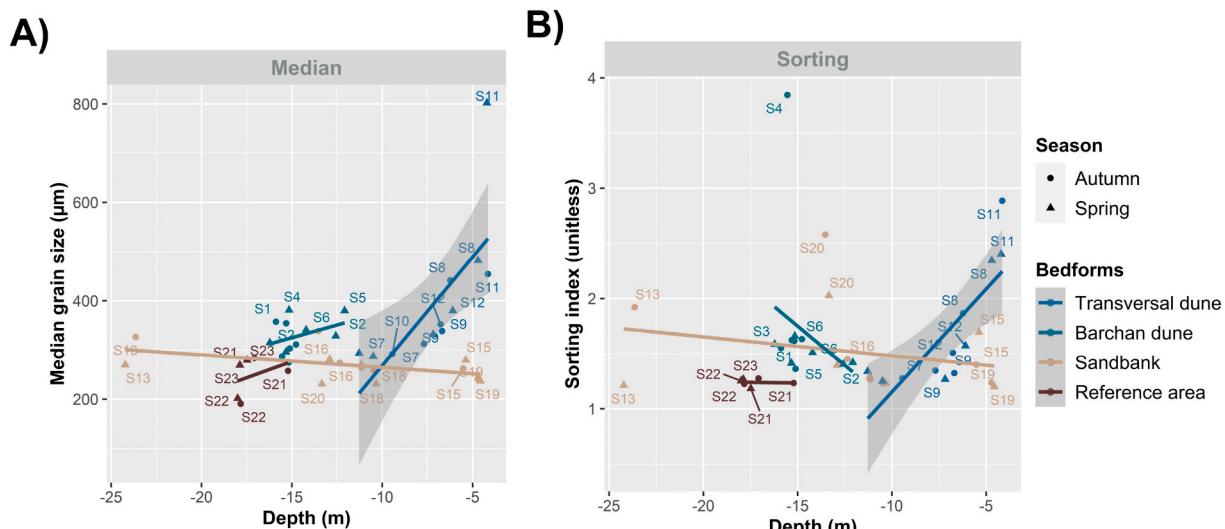


Fig. 4. Relationship between the median grain size (A) and the sorting index (B) against the depth as proxy of the position of the sampling stations within each type of bedform. Significant relationships are represented by a regression line associated with a grey polygon which corresponds to the confidence interval of the regression. Non-significant trends are nonetheless represented but the confidence interval has not been drawn.

Table 3

Main species found within the studied area. Species are ranked according to their relative abundance ("Ab.", %), relative biomass ("Biom.", %) and relative occurrence ("Occ.", %).

Species	Ab.	Biom.	Occ.	Phylum	Main functional characteristics
<i>Lanice conchilega</i>	27	2	57	Annelida	Sedentary deposit feeders or suspension feeders with pelagic eggs and larvae
<i>Spiophanes bombyx</i>	14	0	55	Annelida	Sedentary deposit feeders or suspension feeders with pelagic eggs and larvae
<i>Magelona filiformis</i>	14	1	27	Annelida	Sedentary deposit feeders or suspension feeders with pelagic eggs and larvae
<i>Bathyporeia pelagica</i>	8	1	84	Arthropoda	Small deposit feeders with a direct development or that brood eggs
<i>Hesionura elongata</i>	8	0	27	Annelida	Mobile predator-scavengers
<i>Nephtys cirrosa</i>	7	15	100	Annelida	Mobile predator-scavengers
<i>Capitella capitata</i>	4	1	2	Annelida	Small deposit feeders with a direct development or that brood eggs
Nemertea	4	0	50	Nemertea	Mobile predator-scavengers
<i>Gastrosaccus spinifer</i>	3	2	89	Arthropoda	Mobile predator-scavengers
<i>Liocarcinus</i> sp.	1	0	30	Arthropoda	Mobile predator-scavengers
<i>Salvatoria clavata</i>	1	0	11	Annelida	Mobile predator-scavengers
<i>Urothoe brevicornis</i>	1	0	68	Arthropoda	Small deposit feeders with a direct development or that brood eggs
<i>Ophelia borealis</i>	1	4	66	Annelida	Sedentary deposit feeders or suspension feeders with pelagic eggs and larvae
<i>Bathyporeia elegans</i>	1	0	27	Arthropoda	Small deposit feeders with a direct development or that brood eggs
<i>Nototropis swammerdamei</i>	1	0	25	Arthropoda	Small deposit feeders with a direct development or that brood eggs
<i>Spio martinensis</i>	1	0	39	Annelida	Small deposit feeders with a direct development or that brood eggs
<i>Fabulina fabula</i>	1	1	7	Mollusca	Sedentary deposit feeders or suspension feeders with pelagic eggs and larvae
Others (S = 85)	4	72	Various	Various	Various

value >0.05).

3.3.2. Variability between bedform types

Structural and functional diversities were systematically lower within bedform areas than in the reference area. Indeed, species richness, biomass (Fig. 5) as well as abundance (not shown) were respectively reduced by 23 to 43%, 88 to 92% and 73 to 90%, compared to the reference area. Functional richness and functional redundancy were respectively 39 to 47% and 7 to 31% lower within bedforms. Variations of structural and functional diversities were mostly due to higher biomass of species with pelagic eggs, sub-surface burrowers, sedentary organisms and suspension feeders on the reference area. For instance, the biomass of the echinoderm *Echinocardium cordatum*, the mollusks *Fabulina fabula*, *Donax vittatus*, *Tellimya ferruginosa* and *Euspira catena* was higher within the reference area than within bedform areas.

Structural diversity also displayed a gradient between bedforms: species richness and biomass showed the lowest values on stations located on transversal dunes ($11 \pm 4 \text{ sp} \cdot \text{m}^{-2}$; $1923 \pm 2303 \text{ mg AFDW} \cdot \text{m}^{-2}$) whereas the highest values were recorded on the sandbank ($15 \pm 7 \text{ sp} \cdot \text{m}^{-2}$; $2582 \pm 2556 \text{ mg AFDW} \cdot \text{m}^{-2}$). Functional diversity

exhibited similar variations but this pattern was less clear than for structural diversity (not significant). Multivariate analyses of both species and traits composition (Fig. 6) revealed that these differences were attributable to higher biomass values of mobile predator-scavengers, organisms without structure of protection against physical disruptions, medium sized organisms with a life span of 3–10 years and/or mobile organisms (*Ophelia borealis*, *Glycera lapidum*, *Phyllodocidae*, *Pontocretes altamarinus*) on transversal dunes whereas the sandbank was typified by higher biomass values of deposit-feeders and/or small organisms with a direct development or species that brood eggs (*Bathyporeia pelagica*, *Urothoe brevicornis*, *Bathyporeia gracilis*, *Diastyloides biplicatus*).

3.3.3. Seasonal variability

Structural and functional diversities were generally higher in the spring, relative to autumn (not shown). In spring, species richness increased by 1.7 and 2.1, and abundance by 8.7 and 2.1 on the transversal dunes and the sandbank, respectively. Seasonal variations were mostly due to a higher proportion of juveniles in spring, especially on the reference area (station 22), where juveniles of *Lanice conchilega* thrived ($14,636 \text{ ind} \cdot \text{m}^{-2}$ against a mean of $25 \text{ ind} \cdot \text{m}^{-2}$ in the other

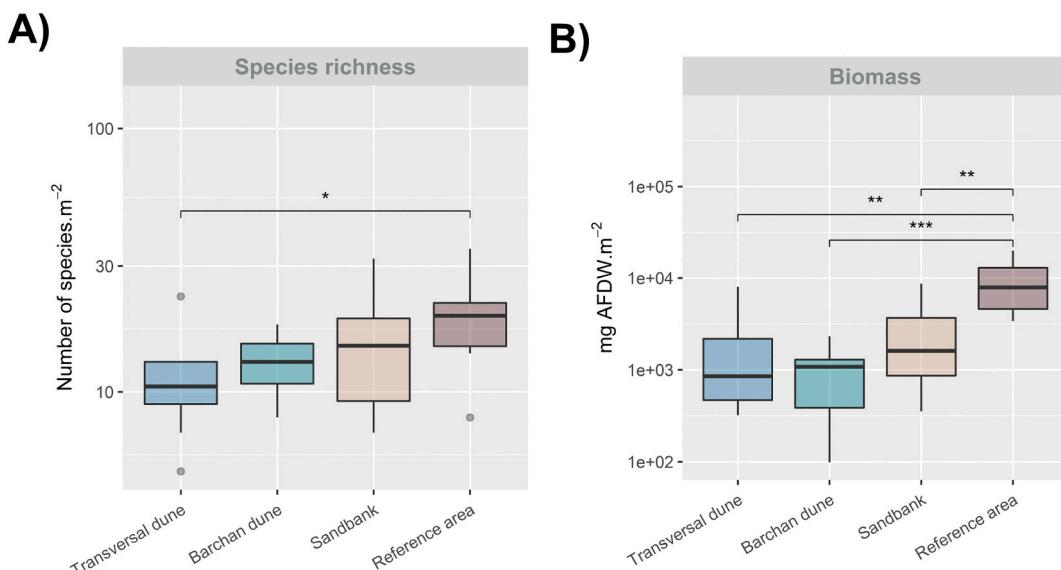


Fig. 5. Distribution of the species richness (A) and of the biomass (B) between the different bedforms and within the reference area. The statistical differences have been assessed thanks to pairwise-Wilcoxon tests. Stars denote the p-value of the tests: “***”: p-value <0.001; “**”: p-value <0.01; “*”: p-value <0.05.

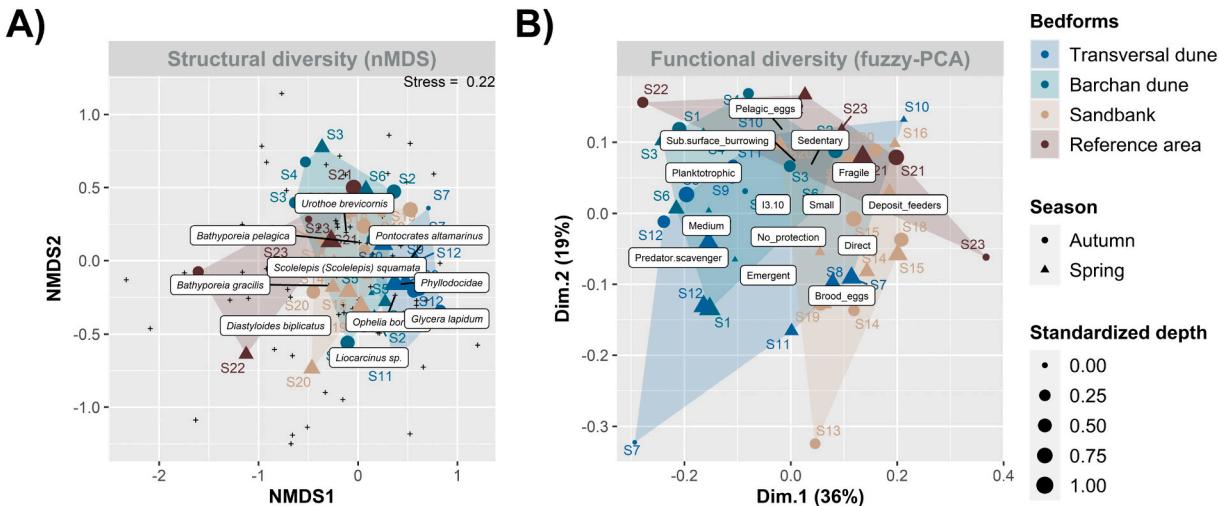


Fig. 6. Variation of benthic communities between the different bedforms, the seasons and the position within a given bedform. A) Non-metric multidimensional scaling computed on the log+1 transformed matrix of species biomass (Bray-Curtis distance; 1000 random permutations). B) Fuzzy-Principal Component Analysis (fuzzy-PCA) performed on the Community-level Weighted Means (CWM) of trait values with log+1 transformed values of biomass as cell values. Only the most important species (as defined thanks to a simper test) and traits are represented.

stations). The biomass of adult was also higher in spring for several species, but deposit-feeders and sedentary organisms such as *Magelona filiformis*, *Hesionura elongata*, *Crangon crangon*, *Spio martinensis*, *Bathyporeia gracilis*, *Eumida sanguinea* and *Salvatoria clavata* contributed the most to the seasonal variations (Fig. 6).

3.3.4. Variation according to the position within a bedform

As shown earlier (see supplementary information S1), depth, as proxy of the position within bedforms, was a poor predictor of macrobenthic communities. Indeed, linear model of regressions showed that only 5 out of 32 relations linking univariate indices of structural and functional diversities to the depth of stations were significant (not shown). Abundance and functional evenness decreased as the depth increased, for barchan dunes and sandbank (p -value <0.001) whereas Pielou's evenness increased with the depth for barchan dunes (p -value <0.01). Surprisingly, functional richness and functional evenness also increased with the depth on the reference area although it was chosen because free from bedforms (p -value <0.05). The R^2 coefficients of determination of these relations varied from 0.65 to 0.82.

Multivariate variations in the species and traits composition between the trough and the crest were relatively difficult to distinguish because variations were weak and subtle, as seen with the Permanova (supplementary information S1). Overall, higher biomass of predator-scavengers, medium sized and/or mobile organisms (such as *Hesionura elongata* and *Salvatoria clavata*) were found at the crest of barchan dunes (Fig. 6). Vertical variations observed within transversal dunes were mostly due to deposit-feeders such as *Echinocardium cordatum*, *Bathyporeia pelagica* and *Urothoe brevicornis*.

3.3.5. Relationships between sedimentary characteristics and benthic communities

Multiple linear models of regression used to link the biotic and the sedimentary characteristics (mud content, median grain size and sorting index) of the studied area explained around 7 to 31% of the variance (see supplementary information S2 for details). The mud content explained between 5 and 31% of the variance in the macrobenthic community structure and functioning and mud was the principal factor responsible for the distribution of the macrobenthic communities. The sorting index and the median grain size were only selected in one (relation with the Pielou's evenness) and three models (relations with the biomass, the multivariate community structure and the CWM), amongst the eight models that were evaluated.

4. Discussion

The Dunkirk area offers the rare opportunity to investigate the structure and the functioning of benthic communities associated with three different sandy bedforms, simultaneously, while avoiding the potential confusion with the effects of other variables such as temperature and salinity. As discussed by Mestdagh et al. (2020), the combination of various sampling methods (multi-beam echosounder, grabs) considerably improved the understanding of seafloor heterogeneity and small-scale distribution of benthic communities. Here, it revealed that the structure and functioning of benthic communities vary according to (i) the type of bedform, (ii) the season and, to a lesser extent, (iii) their location on the dune (from trough to crest). This will constitute a sound basis for environmental impact assessments (e.g. marine aggregate extractions, offshore wind farm developments) and biodiversity management of mobile sand areas (e.g. Marine Strategy Framework Directive) which require information on species distribution and sensitivity to disturbance.

4.1. A benthic community typical of mobile sand areas

Macrobenthic communities of the Dunkirk area are oligospecific, with 14 ± 6 species· m^{-2} , and display low densities (1338 ± 4919 ind· m^{-2}) and low biomass values (2921 ± 4003 mg AFDW· m^{-2}). Methodological differences make it difficult to compare this study results with those reported by Desroy (2002), Cabioch and Glacon (1975) and Davout et al. (1988) in the same area: these authors used a 2 mm sieve mesh (against 1 mm in our study) or a semi-quantitative Rallier du Baty dredge (instead of a Van Veen grab). Nevertheless, results are consistent with those provided by Van Hoey et al. (2004), who set up similar sampling gear near the French-Belgian border: they support the general idea that mobile sands are colonized by a few number of species, adapted and/or specific to frequent disruptions.

Macrobenthic organisms collected within the Dunkirk area are either characteristic of the *Nephthys cirrosa* community, that occurs in well-sorted sandy sediments, or the *Ophelia borealis* community that is typically found in coarse sandy sediments. These two communities were defined by Thorson (1957) for the first time and their distribution is now relatively well mapped, both in the French (Cabioch and Glacon, 1975; Davout et al., 1988; Desroy, 2002) and the Belgian (Breine et al., 2018; Van Hoey et al., 2004) parts of the North Sea.

In this study, macrobenthic communities were mainly dominated by

three annelid species: *Lanice conchilega*, *Spiophanes bombyx* and *Magelona filiformis*. However, this result must be treated with caution and should not be seen as a characteristic of mobile sands habitats. Indeed, the *Lanice conchilega* population was only composed by juvenile individuals and was only observed during the spring survey. In the Elbe estuary, Kühl (1972) found that this species have a relatively long larval phase and spend up to 60 days in the plankton (from April to October). Larvae could thus potentially disperse over a great distance, depending on the hydrographical regime. The distribution of *Lanice conchilega* offshore Dunkirk is probably plethoric and does reflect a well-established population. *Spiophanes bombyx* and *Magelona filiformis* are widely spread across the Belgian Part of the North Sea (BPNS) and the highest densities were found where the median grain size ranged between 100 and 550 µm and/or when the mud content was below 5% (Degraer et al., 2006; Mackie et al., 2006; Meißner and Darr, 2009). At our study site, the dominance of *Spiophanes bombyx* and *Magelona filiformis* was due to their very high densities at the station S22 during the spring survey. This station is located within the reference area, 1 km west of the deposit area for muddy sediments dredged in the Dunkirk harbor (Fig. 1). The local dominance of *Spiophanes bombyx* and *Magelona filiformis* may result from dredging deposition rather than from optimal ecological conditions, as attested by the presence of mud pellets within the sediment sampled at station S22 (Fig. 3). A meta-analysis conducted in England and Wales effectively reported a similar increase in the abundance of both species within the influence area of sedimentary waste (Bolam et al., 2006). The unexpected influence of a deposit area -although relatively far from the station S22- may have compromise the characteristics of the reference area. Caution is thus required when interpreting the differences of both biotic (structural and functional diversity) and abiotic characteristics (sedimentary characteristics) between the bedforms areas and the reference area because the latter is probably not representative enough of a sandy area free from bedforms.

4.2. Sediment movements as an important source of disruption for benthic organisms

It is well known that sediment movements represent a natural source of disruption for macrobenthic organisms by burying them, in the same way as dredging deposition (Bak and Elgershuizen, 1976; Foster et al., 2010; Jones et al., 2016), or by disrupting their metabolism. Indeed, experimental studies revealed that an increase of suspended sediment concentration in the water column can damage the gills of filter feeders and clog their feeding apparatus (Schönberg, 2016; Webster et al., 2017), and thus influence energy, health and reproductive fitness (Bell et al., 2015; Pineda et al., 2016; Schönberg, 2016; Stubler et al., 2015; Tompkins-MacDonald and Leys, 2008; Webster et al., 2017). Finally, the instability of the sediment matrix may prevent sessile species from establishing on mobile sand areas.

The selectivity induced by such environmental constraints is reflected in the trait composition of species within the Dunkirk area. Most organisms are deposit feeders or mobile predator-scavengers. Several species have short life cycles and high productivity, in relation with their small size (Brey, 2001), which allow fast recolonization and the ability to sustain high mortality rates. Moreover, most of the organisms have pelagic eggs and larvae which provide the capacity to avoid the disturbance by living out of the sediment during their first development stages. Some species were also emergent (e.g. *Gastrosaccus spinifer*) and/or sufficiently mobile (e.g. *Bathyporeia pelagica*, *Bathyporeia elegans*, *Urothoe brevicornis*) to avoid burying. Finally, and as observed by Breine et al. (2018) on Belgian dunes, sessile species and suspension-feeders were almost absent from the studied area.

Magnitude of the natural disruptions was uneven within the studied area. The transversal dune can be considered the most impacted with a cumulative rate of migration equivalent to 108 m in ten months. The impact was lower on the barchan dunes, with around 40 m of migration in ten months, and considered null on the sandbank and on the reference

area (see Aernouts, 2005; De Moor, 2002). These variations may then be responsible for the fluctuations in the sedimentary characteristics and for the gradient of structural and functional diversity (i) between the bedforms areas and the reference area, but also (ii) across the various bedforms. Clear gradients of species richness and biomass were effectively recorded between the transversal dune, the barchan dune, the sandbank and the reference area (Fig. 5). Certain studies having investigated the relationships between benthic communities and the type of bedform provided comparable results (Baptist et al., 2006; Ellis et al., 2011; Ferret, 2011). For instance, in the North Norfolk, Ellis et al. (2011) found higher abundances of certain mobile species and/or predator-scavengers (*Bathyporeia elegans*, *Crangon crangon* and *Urothoe brevicornis*) in the sandbank area compared to off-bank sites. Offshore Dieppe (Eastern English Channel), Ferret (2011) observed a decrease in species richness and abundance by a factor 1.5 and 3.5 between a barchan dune composed of sand/gravel and sandy barchan dune with a slight proportion of gravel. The species richness and abundance decreased by a factor 2 between this second kind of dune and a transversal dune constituted by medium to fine sands. Off Tavira Island (southern Portugal), Carvalho et al. (2018) observed that macrobenthic communities located at low depth (7 m) and exposed to intense hydrodynamic conditions and longer period of sediment remobilization displayed low abundance and species richness and were dominated by grazers and suspension feeders. Conversely, at highest depth (22 m) where sediment remobilization was lower, macrobenthic communities were characterized by higher abundance and species richness and were mainly composed of surface deposit-feeders. More generally, results of the present study were consistent with the classic pattern of species/traits succession along natural (van Denderen et al., 2015; Posey et al., 1996) or anthropogenic sources of disruption such as bottom trawling (de Juan et al., 2007; de Juan and Demestre, 2012; van Denderen et al., 2015; Tillin et al., 2006) and metal contamination (Piló et al., 2016). As remembered by Piló et al. (2016), from less disturbed to more disturbed areas, a shift in dominance from carnivore/predators and longer-lived and large animals to the predominance of small size, short-lived and deposit feeders is usually observed.

4.3. Seasonal variability: a minor role of juveniles in the ecosystem functioning?

Our results showed structural and functional diversity increase between autumn and spring. It is well known that benthic communities of the North Sea (Beukema, 1974; Reiss and Kröncke, 2005; Van Hoey et al., 2007) and more generally of the North Atlantic (Dolbeth et al., 2007; Dubois et al., 2009), exhibit a maxima at the end of summer and beginning of autumn and a minima at the end of the winter and beginning of spring. As discussed by Van Hoey et al. (2007), seasonal patterns are due to settlement of larvae and immigration from spring to summer (Beukema, 1974), due to an increase in primary and secondary production within the plankton (Osterman, 1985). The decrease of species richness, abundance and biomass from autumn to winter result from the mortality and emigration of species, for instance to avoid episodic storms which are actually known to alter the macrobenthic communities (Dauer, 1984; Dobbs and Vozarik, 1983; Flint and Younk, 1983; Holland, 1985; Peterson, 1985; Schaffner et al., 1987 in Posey et al., 1996) by influencing bedform dynamics and sediment reworking (Ferret, 2011; Ferret et al., 2010; Le Bot, 2001; Le Bot et al., 2005). Here, spring settlement was reflected by very high densities of juveniles *Lanice conchilega* but also to high abundance of certain species such as *Magelona filiformis*, *Hesionura elongata*, *Crangon crangon*, *Spirio martinensis*, *Bathyporeia gracilis*, *Eumida sanguinea* and *Salvatoria clavata*. These species have also been appointed by several authors to be responsible for seasonal variations of the benthic community structure southern North Sea. In the North Sea, Reiss and Kröncke (2005) and Baptist et al. (2006) also considered that seasonal changes in the benthic community structure were primarily caused by r-selected species such as the polychaete

Spiophanes bombyx or the phoronid *Phoronis muelleri*.

To our knowledge, the functional role of juvenile individuals still remains to elucidate. One can make the assumption that juveniles have a very important, but transient, functional role in spring, for instance by competing with the adults for food and space. But this is probably not the case in mobile sands since a large amount of the ecological niche may remain unavailable because chronic disruptions limit the number of species, the abundance and the biomass. By integrating juveniles in the Biological Traits Analysis (BTA), the present study sheds light on this question. Indeed, juveniles did not emerge clearly in the functional analysis (Fig. 6B), which suggests a limited implication in the overall ecosystem functioning. This analysis was effectively based on the species biomass, following the mass-ratio hypothesis (Garnier et al., 2016) stating that the ecosystem functioning is driven by dominant species, because a larger biomass means a larger utilisation of the available resources (Cadotte et al., 2011). Although juveniles (and especially juveniles *Lanice conchilega*) dominated the abundance of the benthic community, they have a low contribution to the total biomass which explain their minor role in the ecosystem functioning.

4.4. Sediment movements homogenize the benthic community within bedforms

Sedimentary characteristics varied along the slope of the transversal dune and of the sandbank. Nevertheless, while the median grain size increased towards the crest of transversal dunes, which comforted the majority of the observations made on bedforms areas (Baptist et al., 2006; Carvalho et al., 2018; Damveld et al., 2018; Malikides et al., 1989; Mestdagh et al., 2020; Stolk, 2000; Van Lancker and Jacobs, 2000; Wells and Ludwick, 1974), a slight decrease of the median grain size (not significant) was observed between the trough and the crest of the sandbank. Although less documented, this second pattern has however been previously highlighted by Davout et al. (1988) in the Dunkirk area, but also by De Maeyer and Wartel (1988), Ferret (2011) and Harvey (1966) at various sites. The distribution of the sediment characteristics between the trough and the crest must be connected to the orientation of bedforms. Indeed, transversal dunes being perpendicular to the tidal current, the depressions act as traps for finer sediments, but also for pebbles (Dyer, 1971). Conversely, the sandbank being parallel to the main tidal currents, hydrodynamics is reinforced in the troughs which, in turn, may induce the advection of the fine sedimentary particles. Depressions separating sandbanks then shelter coarse sediments (as observed at station S17).

Variations of sedimentary characteristics within bedforms are generally reflected in the macrobenthic community structure which similarly differs along the slope of bedforms (Damveld et al., 2018; Ellis et al., 2011; Van Dijk et al., 2012). Indeed, Damveld et al. (2018) showed, from a video survey, that the density and the number of epibenthic organisms were respectively 30 and 4 times higher in the trough than on the crest of sand ripples (small bedforms with a wavelength <60 cm and with a height <6 cm). Ferret (2011) found a higher abundance of mobile organisms and/or predators-scavengers (e.g. *Gnathia* sp., *Aphessa bispinosa* and *Galathea intermedia*) at the crest of the dunes where these organisms may find favorable conditions to ambush. Nevertheless, Ferret (2011) remarked that this scheme is not universal: the distribution of benthic communities can be bedform-specific. In our study, structural and functional diversity did not show any clear trend along the sandbank and the transversal dune profiles. This result can be explained by two hypotheses. First, although a gradient in the sedimentary characteristics has been observed, it could be insufficient to have a significant influence on the distribution of macrobenthic organisms (the median grain size ranged approximately from 250 to 300 µm on the sandbank and between from 300 to 450 µm on the transversal dunes). Secondly, it is possible that the strong sediment movements on the transversal dune induce small-scale homogenization of the benthic fauna within bedforms.

Unexpected relationships between the biodiversity and the depth of sampling stations were found on barchan dunes and on the reference area, despite low gradients of depth and without drastic consequences on the distribution of macrobenthic communities. As seen on the high-resolution bathymetric maps (Fig. 2) small dunes and ripples were locally superimposed on the dunes, sandbank and reference areas. It is then possible that these small bedforms were responsible for the unexpected relationships with depth, as shown by Baptist et al. (2006) and Damveld et al. (2018) studying sandbanks of the North Sea. Microscale studies must be considered in order to resolve this issue.

4.5. An ecosystem adapted to anthropogenic disturbances?

The present study provides evidence that sediment movements associated with bedform migrations are responsible for the spatial (between bedforms) variations of benthic communities and to their homogenization over the slope of the bedform. It nuances the ecological theory arguing that spatial heterogeneity of the habitat promotes a certain degree of local diversity by generating a higher number of ecological niches (MacArthur and Wilson, 1967; Thrush et al., 2006; Tilman, 1982): biodiversity improvement can be only expected if topographic features are stable, both in space and time.

In this context of high levels of natural disturbance, one can wonder about the potential impact of human activities reworking the seabed of bedforms areas, for instance considering the installation of power cable connecting offshore windfarms to the grid (ploughing, jetting and cutting-wheels; see the review by Taormina et al., 2018) or for the extraction of marine aggregates (Birchenough et al., 2010; Cooper et al., 2007; Krause et al., 2010; Ferret et al., 2010). Following a trait-based approach, van Denderen et al., 2015 found that natural (bed-shear stress) and anthropogenic disturbances (bottom trawling) induce a similar selection of biological traits. As a consequence, there was no detectable effect of bottom trawling on benthic communities exposed to high natural disturbance. As seen above, the traits composition in the Dunkirk area was very similar to trait composition reported from areas exposed to anthropogenic disruptions. Species could be able to avoid, to sustain and to recover quickly after a physical disturbance event. Moreover, although variations between bedforms areas and the reference areas exist, there was a relatively high degree of overlap between the different communities. Given all these elements, one may confidently predict that human activities on mobile sand areas may have a limited impact, both in space and time.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2021.112695>.

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