

Dynamic of the benthic ecosystem of bedform areas assessed via structural diversity, functional diversity and isotopic diversity

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ABSTRACT: Thanks to the combination of various measures of diversity (structural diversity, functional diversity and isotopic diversity) the present study investigates the spatio-temporal dynamic of the benthic ecosystem of bedform areas. Results suggest that the macro-scale distribution of species 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. Conversely, the high frequency of migration events homogenizes macrobenthic communities between the troughs to the crest of bedforms. The benthic community structure also changes between seasons due to the massive recruitment of juveniles. However, if species identity and structural diversity change it have little consequences on the general ecosystem functioning. Especially, the benthic food web of bedforms areas appears very stable with limited variations, both in space and time. It displays very simplistic trophic pathways, and the present study confirms the major role of Phytoplankton blooms (and especially *Phaeocystis*) in sustaining the benthic food web.

As bedform areas are targeted for the installation of offshore windfarms, this study will provide a sound scientific basis for future impact assessments.

1 INTRODUCTION

The French continental shelf and especially the Dover straight, the western English Channel, and the Iroise and Celtic Seas exhibit sandy bedforms such as sandbank, dunes and ripples (see the

classification of subaqueous bedforms by Ashley, 1990). These structures differ in their morphology (Aernouts, 2005; Le Bot, 2001; Le Bot et al., 2005; Van Lancker et al., 2009) but also in their dynamic: whereas sandbanks are stable over hundreds of years, subtidal dunes are 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).

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: a *Nephtys cirrosa*/*Ophelia borealis* community found in medium to fine sand assemblage, and a *Magelona johnstoni*/*Hesionura elongata* community on muddy heterogeneous sediments. In the French part of the North Sea, these communities exhibit a remarkably low diversity and density with respectively 4.7 and 11.7 species.0.5 m⁻² as well as 19.2 and 113.4 ind.0.5 m⁻² (Desroy, 2002).

At a smaller spatial scale, certain studies revealed a decrease in species richness, abundance and Shannon's diversity 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; Ferret, 2011; Mestdagh et al., 2020; van Dijk et al., 2012). These studies were based on taxonomic approaches and, *de facto*, did not consider the role played by species in the ecosystem. More generally, the benthic ecosystem functioning, and especially trophic relations, are poorly known on bedform areas.

Thanks to various measures of biodiversity (structural diversity, functional diversity, and isotopic diversity) the present study aims at improving the knowledge on the dynamic of the benthic ecosystem on bedforms areas.

2 MATERIAL & METHODS

2.1 Study area

The present study focused on an 80 km² area located within the French Flander bank, offshore the Dunkirk harbor (Figure 1). 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.

2.2 Sampling strategy

Biological material was collected according to a stratified sampling design (Figure 1). Samples were performed (i) in a coastal area with barchan dunes (crescent-shaped dunes), (ii) a transitional area with transversal dunes (*i.e.* straight-lined dunes) and (iii) an offshore area with a sandbank.

Macrobenthic organisms were collected via 23 stations distributed between the trough, the slope and the crest of each bedform (and not only sandbanks). Three additional stations were positioned within a reference area, free from bedforms. Three replicates were collected at each sampling station using a Van Veen grab (0.1 m²), approximately with a 5–10 m accuracy in the positioning (the vessel size was 20 m length overall). One sub-sample has also been extracted at each station for grain size analysis.

This sampling strategy has been reproduced in autumn 2019 and spring 2020 in order to assess the temporal dynamic of the ecosystem.

2.3 Material collection for stable isotopes analysis

At each sampling station, one additional grab sample has been collected in order to analyse the stable isotope signatures of macrobenthic organisms. In order to provide a larger insight about the benthic food web, 26 trawl hauls (commercial trawl with a “Grande Ouverture Verticale”) were also performed on the coastal, the transitional and the offshore area (Figure 1). The cod-end mesh was reduced to a 20 mm mesh-size (stretched) in order to improve the catch of juvenile fish and megabenthic species.

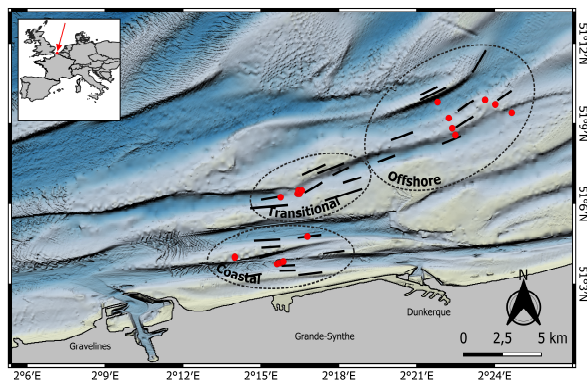


Figure 1 Map of the study area. Red dots represent the location of grab samples whereas black lines represent the location of trawl hauls. Source of data : Shom, 2016. MNT topo-bathymetrique côtier à 20m du détroit du Pas-de-Calais (Projet TANDEM).

A total of 37 species contributing to almost 90% of the biomass was selected for stable isotopes analysis. A maximum of 5 sub-samples per species and size class was dissected at each zone. Samples consisted of muscle tissue for fish and large organisms (bivalves, crustaceans) whereas the entire organism's body was used for the smallest species (small annelids).

Stable isotope signatures of potential sources of carbon and nitrogen were gathered from an aliquot of sediment, extracted from grab samples (Sedimentary Organic Matter; SOM) and by filtering 500mL of water on a GFF filter thanks to a Niskin bottle (Particulate Organic Matter, POM).

Samples processing for stable isotope analysis was similar to the method described in Quillien et al., (2016).

The $\delta^{13}\text{C}$ values as a proxy of food source (Bearhop et al., 2004; Post, 2002) and $\delta^{15}\text{N}$ values as proxy of the trophic position (Hussey et al., 2014; Post, 2002) were determined by weighting the $^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$ ratio of a sample relative to the $^{13}\text{C}:^{12}\text{C}$ ratio in a standard (Vienna Pee Dee Belemnite for carbon and N_2 in air for nitrogen) :

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 10^3$$

with R corresponding to the ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$.

2.4 Data analysis

Structural diversity, functional diversity as well as isotopic diversity were assessed thanks to a combination of multivariate analysis (non-metric MultiDimensional Scaling, fuzzy Principal Component Analysis and $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ biplot) and univariate indices (see Table 1).. Biological traits scores used to assess functional diversity have been published as open access database in the SEANO portal (Robert et al., 2021. doi:10.17882/80785).

Table 1 Univariate indices used to assess structural diversity, the functional diversity as well as the isotopic diversity of bedform areas

Diversity	Univariate indices	References
Structural diversity	Species richness (S)	Shannon and Weaver (1949) Pielou (1966)
	Shannon's diversity (H')	
	Pielou's evenness (J')	
	Total abundance (Ab.) Total biomass (Biom.)	
Functional diversity	Functional Richness (FRic)	Villéger et al. (2008) van der Linden et al. (2012)
	Functional Evenness (FEve)	
	Functional Divergence (FDiv)	
	Functional Redundancy (Fred)	
Isotopic diversity	$\delta^{13}\text{C}$ range (CR)	Layman et al. (2007) Cucherous set and Villéger (2015)
	$\delta^{15}\text{N}$ range (NR)	
	Isotopic Richness (IRic)	
	Isotopic divergence (IDiv)	
	Isotopic dispersion (IDis)	
	Isotopic evenness (IEve) Isotopic uniqueness (IUni)	

3 RESULTS-DISCUSSION

3.1 Spatio-temporal variations of benthic communities

Benthic communities are shaped by sediment movements - 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 (Foster et al., 2010; Jones et al., 2016), or by disrupting their metabolism. 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,

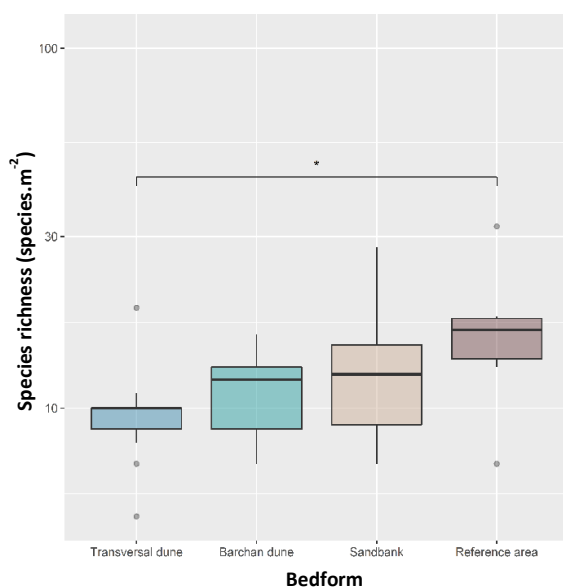


Figure 2 Distribution of the species richness between the different bedforms and within the reference area. Statistical differences have been assessed thanks to pairwise-Wilcoxon tests. Stars denote the p-value of the tests: “***”: p-value <0.001; “**”: p-value <0.01; “*”: p-value <0.05.

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 (not shown). 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. These differences were reflected in the species richness (Figure 2) and biomass that showed a gradient between bedforms. To our knowledge, no additional studies investigated how structural and functional diversity vary with the kind of bedform.

A classical pattern of seasonal variability - Structural diversity and to a less extent, functional diversity, were generally higher in spring, relative to autumn. For instance 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. Spring settlement was reflected by very high densities of juveniles *Lanice conchilega* but also by higher abundance of small species such as *Magelona filiformis*, *Hesionura elongata*, *Crangon crangon*, *Spio martinensis*, *Bathyporeia gracilis*, *Eumida sanguinea* and *Salvatoria clavata*. This was consistent with several studies conducted in the North Sea where benthic communities exhibit a maximum at the end of summer and beginning of autumn due to settlement. They show a minima at the end of the winter and beginning of spring due to immigration and high mortality rates (Reiss and Kröncke, 2005; Van Hoey et al., 2007).

Sediment movements homogenize the benthic community within bedforms -- Sedimentary characteristics varied along the slope of the transversal dune and of the sandbank (Figure 3). The median grain size increased towards the crest of transversal dunes, which was consistent with previous studies (Carvalho et al., 2018; Damveld et al., 2018; Mestdagh et al., 2020), probably because transversal dunes are oriented perpendicular to the tidal current which induces a trap of fine sediment in inter-dunes depressions. Conversely, a very slight decrease of the median grain size (not significant) was observed between the trough

and the crest of the sandbank (Figure 3). This bedform is oriented parallel to the main tidal currents. Bed shear stress could be stronger in inter-banks depressions, which, in turn, may induces the advection of fine sedimentary particles.

Variations of sedimentary characteristics within bedforms did not alter the structural and functional diversity along the slope of the sandbank and dunes. This result differs from those obtained by a few rare studies performed on this topic, revealing a higher benthic diversity in the trough compared to the crest of bedforms (Damveld et al., 2018; Ellis et al., 2011; van Dijk et al., 2012). did not show any clear trend along the sandbank and the transversal dune profiles which differ from previous studies. It is hypothesized that natural sediment reworking induces a small-scale homogenization of macrobenthic communities within bedforms of the Dunkirk area.

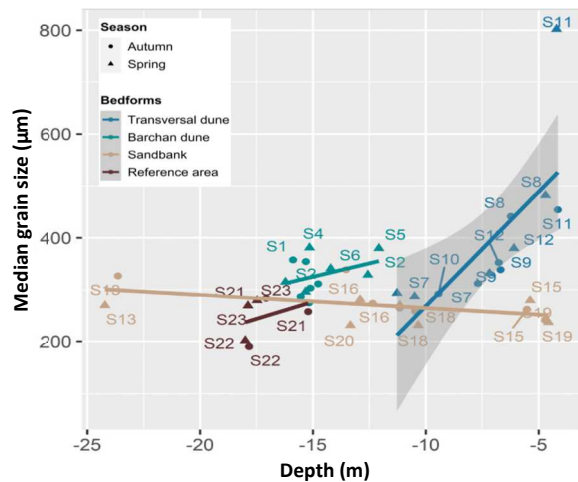


Figure 3 Relationship between the median grain size against the depth as proxy of the position of the sampling stations within each type of bedform. Significant relationships are represented by a regression line associated with a grey polygon which corresponds to the confidence interval of the regression. Non-significant trends are nonetheless represented but the confidence interval has not been drawn.

3.2 Dynamic of the benthic food web

A simple food web structure - Stable isotopes analysis revealed a very simplistic but particular food web, composed by four trophic guilds only: (i) deposit feeders, (ii)

filter feeders/deposit feeders, (iii) small benthic predators and (iv) large predators. This simple structure is in accordance with the low diversity of bedform areas (14 ± 6 macrobenthic species per m^{-2} at Dunkirk).

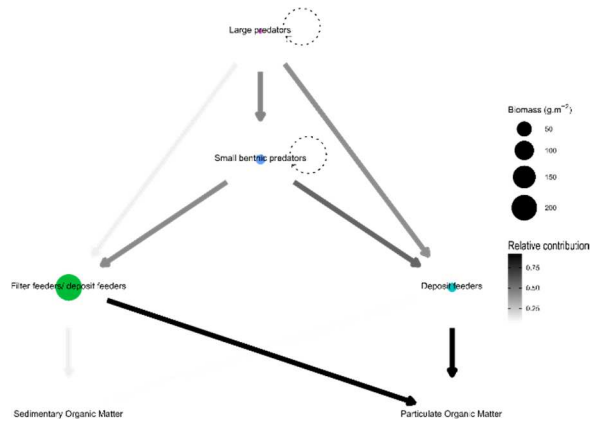


Figure 4 Schematic representation of the benthic food web of subtidal sand dunes. Width of arrows are proportional to the contribution of each food source in the diet of each consumer multiplied by the relative biomass of consumers to provide an idea about trophic fluxes.

Importance of the benthopelagic coupling - In the study area, the organic matter content in the sediment remains below 0.5% (not shown) so that the benthic organisms may have been adapted to feed on other source. Effectively, outputs of mixing models clearly suggest a strong benthopelagic coupling, with POM contributing to more than 80% in the diet of primary consumers (deposit feeders and filter feeders/deposit feeders). The southern North Sea is typified by major phytoplankton blooms where *Phaeocystis globosa* is often the dominant species (Karasiewicz et al., 2018; Karasiewicz and Lefebvre, 2022; Lefebvre and Dezécache, 2020). As *Phaeocystis* represents an important part of POM, it is thus very likely to sustain the benthic food web of sandbanks, as described by Franco et al. (2008) in the Southern Bight of the North Sea.

Temporal variations in the signature of the main food source – A decrease in the mean values of $\delta^{13}C$ of POM has been observed between autumn and spring. It may result from the selective consumption of

Dissolved Inorganic Carbon by phytoplankton cells (the ^{12}C is primarily consumed while the ^{13}C accumulates) during the growth period, and/or a switch toward the utilization of HCO_3^- instead of CO_2 when the latter is depleted (France et al., 1997; Leggett et al., 2000, 1999). Conversely, the $\delta^{15}\text{N}$ decreased in spring due to a possible shift of dominant species in the plankton community with a larger proportion of heterotrophic organisms (Aberle et al., 2010; Agurto, 2007).

The structure of the food web remain relatively stable between seasons - A significant decrease in the range of $\delta^{13}\text{C}$ has been observed between autumn and spring but seasonal variations decreased as the trophic level of trophic guilds increased (Figure 5). This result suggests the utilization of a narrower spectrum of food sources (Layman et al., 2007). Here it may reflect a larger contribution of POM in the diet of primary consumers during *Phaeocystis* blooms, which, in turn may cascade in the rest of the food web. Despite this, the $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ biplot remained relatively similar between autumn and spring (not shown), which suggests that no particular shift in the diet of trophic guilds occurred and that the higher diversity found in spring (see paragraph 3.1) has little impact on trophic relationships. This result is probably due to the remarkably low diversity of bedform areas (whatever the season), which limit the number of possible trophic pathway.

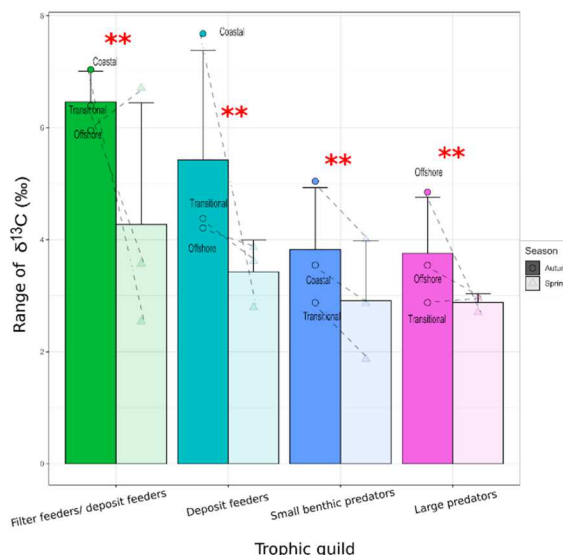


Figure 5 Spatio-temporal variations in the values of isotopic diversity indices for each trophic guild. Statistical differences have been assessed thanks to pairwise-Wilcoxon tests. Stars denote the p-value of the tests: “***”: p-value <0.001; “**”: p-value <0.01; “*”: p-value <0.05.

4 CONCLUSIONS

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. However, if species identity vary to some extent in space and time, the ecosystem functioning, and especially trophic relationships, remains relatively stable with only with minor variations.

5 ACKNOWLEDGEMENTS

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