Ecological Indicators 146 (2023) 109854

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Functional trait responses to different anthropogenic pressures

Felien Festjens[a,*], Jolien Buyse[a], Annelies De Backer[a], Kris Hostens[a], Nene Lefaible[b], Jan Vanaverbeke[c], Gert Van Hoey[a]

[a] Flanders Research Institute for Agriculture, Fisheries and Food (ILVO), ILVO-Marine, Jacobsenstraat 1, 8400 Oostende, Belgium
[b] Ghent University, Biology Department, Marine Biology Research Group, Krijgslaan 281/S8, 9000 Gent, Belgium
[c] Royal Belgian Institute of Natural Sciences, Operational Directorate Natural Environment, Marine Ecology and Management, Vautierstraat 29, B-1000 Brussels, Belgium

A R T I C L E I N F O

Keywords:
Anthropogenic pressure
Macrobenthos
Functional diversity
Functional correspondence analyses
Environmental impact assessment

A B S T R A C T

There is an increasing awareness that knowledge of the functional diversity of a community is key to understand how the community responds to environmental and anthropogenic pressures. The Belgian Part of the North Sea (BPNS) represents a highly dynamic area that is subject to a variety of human activities. The main objective of this study is to investigate the usefulness of functional diversity indices and fuzzy correspondence analysis (FCA) to evaluate their applicability in assessing changes in benthic functional properties in the frame of environmental impact assessments (EIAs) for dredge disposal, sand extraction and offshore wind energy exploitation. Ten traits were selected, subdivided in 47 modalities, including both response- and effect traits. Functional diversity was quantified through different functional indices while shifts in trait composition due to anthropogenic pressure were determined by FCA. The analyses were based on a benthic dataset of 1262 samples.

Results revealed that under chronic pressure of high disposal or sand extraction, the functional diversity indices – especially functional richness - showed a clear response. However, considerable variation (decrease/increase) was found for the index values between the impacted sites. Within the offshore wind farms, findings for the functional diversity indices were less pronounced. The FCA graphs revealed a shift in trait composition in all cases except for *Macoma balthica* and *Nephtys cirrosa* habitat in the dredge disposal case.

The BPNS - with different types of pressure and levels of impact - provided the ideal platform to assess the potential of biological trait-based indicators. While responses are complex and dependent on several aspects such as local habitat, pressure type or level of impact, our results proved that functional trait analyses are a necessary and complementary tool in future environmental impact assessments.

1. Introduction

The marine environment is under pressure due to its intensified use as a mode of transportation and a source of raw materials, food and energy (Halpern et al., 2008). On top of that, marine environments also suffer from the consequences of climate change and eutrophication (Chapman, 2017; Harley et al., 2006). Keeping track of the sensitivity and resilience of the marine environment and its communities is essential to safeguard the provisioning of marine ecosystem services.

The Belgian part of the North Sea (BPNS) offers a perfect study area to compare the degree of (localized) impact of three different physical human activities on the benthic ecosystem: i.e. dredge disposal, sand extraction and offshore wind energy exploitation. At the BPNS, these activities are allocated to specific areas and tracked by dedicated monitoring programs, as regulated by different ministerial and royal decrees (Douvere et al., 2007; Verhalle, 2020). Dredge disposal may result in a shift in community composition and reduced diversity, albeit with the response varying according to the amount, nature and frequency of disposal and the nature of the receiving environment (Bolam, 2011; Bolam et al., 2006; Van Hoey et al., 2022). Sand extraction may also cause local biodiversity decreases (Cooper et al., 2007), although opposite trends have been observed as well at high extraction intensities (De Backer et al., 2014a,b). Moreover, extraction regime and local geological context are important factors driving the environmental impact of sand extraction on tidal sandbanks (Wyns et al. 2021). Research on offshore wind farms (OWFs) has also recorded variable effects on the surrounding soft-sediment infaunal communities, depending on the technical attributes of the OWF and site specific

* Corresponding author.
E-mail address: felien.festjens@ilvo.vlaanderen.be (F. Festjens).

https://doi.org/10.1016/j.ecolind.2022.109854
Received 9 September 2022; Received in revised form 22 December 2022; Accepted 29 December 2022
Available online 4 January 2023

baseline conditions (Lefaible et al., 2018; Lefaible et al. submitted). Increased macrofaunal densities and diversity were observed at immediate (<15 m, Coates et al., 2014) and nearby (37.5 m, Lefaible et al., 2018) distances from the turbines within the transitional OWF, C-Power. These infaunal responses have been attributed to the “artificial reef” effect, caused by altered hydrodynamics and knock-on effects (biodeposition and drop-off) by the colonizing epifaunal communities within the surrounding sediments (Degraer et al., 2020, Lefaible et al. submitted).

De Backer et al. (2014a) found similar diversity-disturbance responses of the macrobenthos to all three activities, indicating that the different pressures of these activities have induced similar environmental changes on the soft-sediment macrobenthos related to fining of the sediment, smothering and abrasion (Bolam et al., 2016; Tillin et al., 2006). While these studies highlight the importance of investigating the structural diversity, there is an increasing awareness that knowledge of the functional diversity of a community is equally important to understand how the community responds to environmental and anthropogenic pressures (Gogina et al., 2014; van der Linden et al., 2012). Whereas structural diversity is merely based on the taxonomic identities of the community, functional diversity focuses on their contribution to ecosystem functioning (Mouillot et al., 2013). Structural measurements such as the number of species maintained by a community may be incorrectly interpreted as a sign of ecosystem recovery if the new species do not fulfill the same functional role as their predecessors Villéger et al., 2010).

In biological trait analysis (BTA), differences in benthic communities are not based on taxonomic differences but on differences in morphology, behavior and other life history characteristics (Andersen et al., 2016; Beauchard et al., 2017; Bremner et al., 2003, 2006a, 2006b). Several studies also stress the need to differentiate between effect traits and response traits; response traits being those which respond to the pressure and effect traits those who are associated with the shift and have a functional effect, but not actually directly responding to the pressure itself (Bolam et al., 2016, 2021; Hooper et al., 2005). Response traits can be especially relevant in assessing species thresholds and the resilience of ecosystems to change (Gutt, 2017). BTA enables us to detect potential changes in ecosystem functioning when a pressure increases, with e.g. a decrease in trait characteristics (modalities) that are sensitive to pressures. For instance, Bolam et al. (2016) reported that the crustose, tunicate and surface-dwelling macrobenthic taxa were response traits particularly sensitive to dredge disposal, while the altered community had a greater bioturbatory capacity thanks to a domination of the effect trait modalities surface deposition and diffusive mixing bioturbation.

The main objective of this study is to investigate the usefulness of functional diversity indices and fuzzy correspondence analysis, a multivariate (visual) tool to evaluate their applicability in assessing changes in benthic functional properties in the frame of environmental impact assessments (EIAs) for dredge disposal, sand extraction and offshore wind energy exploitation. This is done using a large benthic dataset (1262 samples), which is spread over the activities and the different habitats with their associated macrobenthic communities (Breine et al., 2018). This allows also to perform a habitat dependency evaluation, where the local habitat conditions are considered in the assessment. The applicability is evaluated based on the following research questions: (1) do the functional diversity indices respond to the human activities and if so, in what way, (2) what are the most impacted traits, and (3) are the pressure-induced functional responses site or case-dependent?

2. Material & methods

2.1. Study area and human impact history

The Belgian Part of the North Sea (BPNS) spans around 3500 km^2 with 65 km of coastline, is relatively shallow (on average 20 m deep), characterized by different macrobenthic communities (Breine et al., 2018), and intensively used. For this study, we focus on three human activities: dredge disposal, sand extraction and offshore wind energy exploitation (Fig. 1). These activities are executed in specific zones as indicated in the Belgian Marine Spatial Plan (Douvere et al., 2007; Verhalle, 2020).

Dredge disposal is licenced at five sites (Br&W S1 [LS1], Br&W S2 [LS2], Nieuwpoort [NWP], Br&W Zeebrugge-East [ZBO] and Br&W Oostende [OST]) within the coastal area of the BPNS (Fig. 1). LS1 and NWP are considered *Abra alba* habitat, while ZBO and OST are *Macoma balthica* habitat. Although structurally different, they both mainly consist of sessile, tube building and burrow dwelling macrobenthic species that live in a muddy to fine muddy sand-habitat (Breine et al., 2018). LS2 on the other hand is part of the *Nephtys cirrosa* habitat, with medium sand and inhabited by free-living, mobile species with a short lifespan (Breine et al., 2018). Information on dredge disposal intensity of the period 2006–2016 was obtained from the Maritime Access Division of the Flemish Government, measured as total tons dry matter yearly disposed (Lauwaert et al., 2019). This has shown that dredge disposal mainly occurs at sites LS1, ZBO and LS2 (on average 5.1, 3.3 and 2 million tons per year, respectively) on a continuous basis. A low disposal activity occurs at OST, with on average 0.5 million tons per year in certain periods throughout the year. At NWP, on average only 0.1 million tons per year are disposed, mainly once a year.

Sand extraction is restricted to several dedicated concession zones within the BPNS, of which three subzones are included in this study (Fig. 1). These zones are situated in originally similar sedimentary areas i.e. dominated by medium sands (250–500 µm) (Verfaillie et al., 2006). These areas are considered *Hesionura elongata* habitat, inhabited by short- and free-living, mobile species, and displaying a high taxon richness (Breine et al., 2018). The Buiten Ratel (zone 2b) used to be the most intensive area of extraction between 2008 and 2014, with a total sand removal of about 11.6 million m^3 (Roche et al., 2017). After closure of the central zone in January 2015, dredging activity shifted almost completely towards the Thorntonbank (zone 1a), that has been subjected to a steady increase in extraction pressure since 2010. By 2016, the cumulative volume of extracted sand reached 10 million m^3, making this area the epicenter of industrial sand extraction in more recent years (Roche et al., 2017). Extraction on the Hinderbanken (zone 4c) started in 2012 and has shown peaks during a couple of months of the year followed by months without extraction. In 2014, for example, a substantial extraction peak of 2.6 million m^3 took place (mainly for beach nourishment) of which more than half of this volume was extracted within 2 months (Roche et al., 2017).

The concession zones for offshore wind energy exploitation are located in the eastern part of the BPNS, adjacent to the Dutch border (Fig. 1). Several offshore wind farms (OWFs) are currently operational, but this study focuses on two OWFs which differ in terms of distance from the coastline, timing of construction and turbine types (Rumes & Brabant, 2017). The C-Power OWF is located on the Thornton Bank at approximately 30 km from the Belgian coastline. This park was the first to be constructed during two separate phases: in 2008 six gravity-based foundation were built, followed by 48 jacket foundations in 2011–2013 (http://www.c-power.be). The Belwind OWF is located on the Bligh Bank at approximately 46 km from the coastline and construction activities started in 2009, resulting in a total of 55 operational turbines built on monopile foundations by 2011 (Rumes & Brabant, 2018). Both parks contain habitats that can be categorized as high-energy environments with well-sorted, medium-coarse sands and low organic matter contents (Van Hoey et al., 2004). The associated macrobenthos within these soft-sediments have moderate to low values in terms of densities and richness, that are mainly comparable to the widespread, transitional *Nephtys cirrosa* assemblage (Breine et al., 2018; Van Hoey et al., 2004).

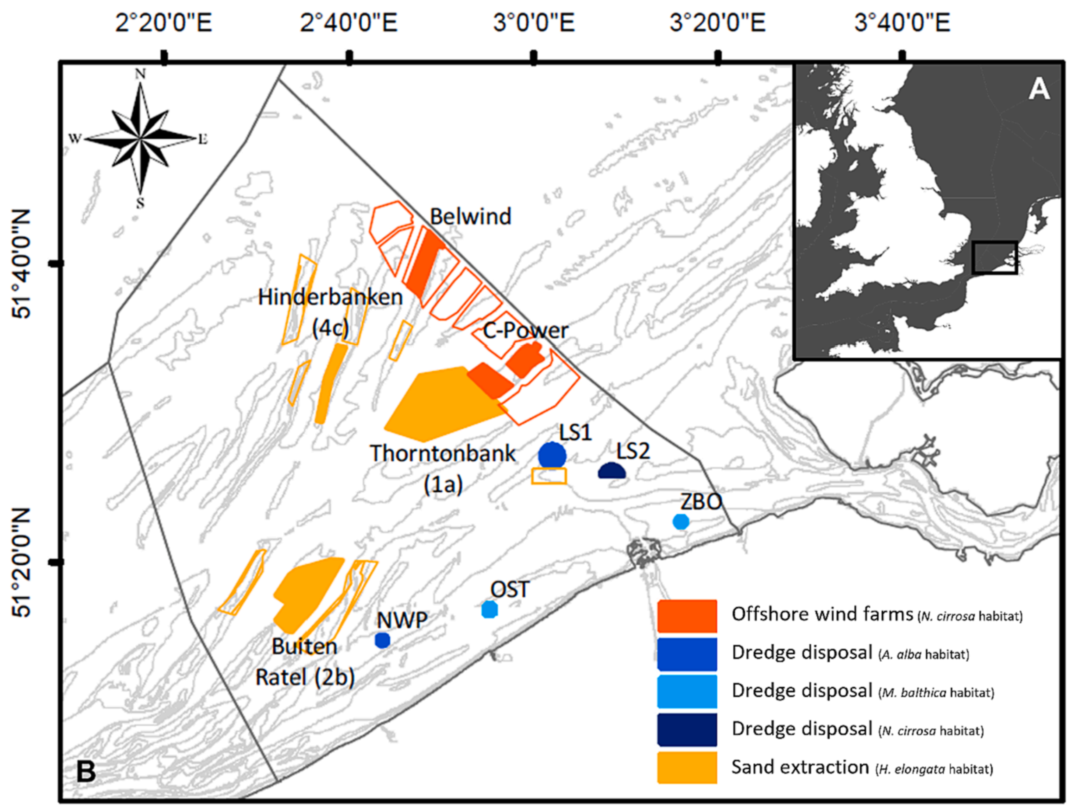


Fig. 1. Overview map with A) location of the Belgian part of the North Sea (BPNS), B) locations of the three studied human activities in the BPNS, the habitat types are mentioned in the legend. All of the sand extraction zones and offshore wind farm concessions are shown on the map, when falling outside the scope of this study, only the contours are shown. The contours of the sand banks are depicted in light grey.

2.2. Sampling strategy and data availability

Despite differences in terms of sampling strategy and data availability, actual sample collection and treatment was balanced between the three studied impacts (Annex A1). Macrobenthos samples were obtained by means of a Van Veen grab (0.1 m^2, one sample per sampling site) each year during autumn (September-October). Samples were sieved over a 1-mm sieve, stained with Rose Bengal/eosin to facilitate further sorting, and preserved in approx. 6 % formaldehyde-seawater solution. Macrobenthic organisms were sorted, counted and identified to species level where possible.

For each case, an impact-control sampling strategy was followed, where the control sites were chosen to resemble the physical environment of the impact sites and at the same time they were located outside of the area of influence of the activity. For the dredge disposal case, a long-term time series (2007–2016, 635 samples in total) of macrobenthic data was available for the five disposal sites (Van Hoey et al., 2022). The number of sampling sites per disposal area changed over the years. The most intensively used disposal sites (LS1, ZBO and LS2) have been sampled yearly, while NWP and OST were sampled at least once every 3 years since 2011. For the sand extraction case, 442 samples have been taken in the period 2009–2016 spread over the three studied concession zones (Buiten Ratel (BR; BRM & BRC), Thorntonbank (TB) and Hinderbanken (HB; zone 4c))(De Backer et al., 2017). Data for wind energy exploitation activities were obtained within C-Power and Belwind in the years 2017–2018. In total, 185 samples were taken, with impact samples taken at 37.5 m distance from the turbine center, and control samples collected at 350–500 m distance from any surrounding turbine (Lefaible et al., 2018, 2019).

2.3. Data analyses

2.3.1. Biological traits

Ten relevant biological traits (Lam-Gordillo et al., 2020) were selected and subdivided into 47 modalities following Breine et al. (2018) (Table A1). As suggested by Bolam et al. (2016), those traits were classified in two categories: five response traits (morphology, egg development, living habit, sediment position and mobility) and five effect traits (maximum size, longevity, larval development, feeding mode and bioturbation). A list of the traits and their modality labels is given in Annex A2.

Each taxon was assigned to the trait categories using a 'fuzzy coding' approach (Chevene et al., 1994), using the Cefas traits information (Clare et al., 2022). The trait categories were given an affinity score between 0 and 3, with 0 indicating no affinity and 3 indicating a high affinity of a species to a trait category. The fuzzy coding procedure allows to capture the variability in affinity, thereby addressing spatial or temporal variation in the traits per taxon (Statzner & Bêche, 2010). To give the same weight to all taxa and each trait in further analysis, the scores were standardized so that the sum for a given taxon and a given trait equaled 1 (or 100 %). Biological traits analyses were performed by weighing traits against species abundances (van der Linden et al., 2012). Therefore, the resulting species-by-trait matrix was combined with the species abundance-by-sample matrix to create the final sample-by-trait matrix that was used to calculate the functional diversity indices (Beauchard et al., 2017). For the fuzzy correspondence analyses, the abundance-by-sample matrix has prior been Hellinger-transformed to avoid problems associated with potentially low counts and many zeros (Legendre & Gallagher, 2001).

2.3.2. Functional diversity indices

All calculations on functional diversity (FD) were carried out in R (R

Core Team, 2020) with the FD software of Laliberté & Legendre (2010). The software calculates a range of multidimensional indices, based on principal co-ordinates analysis (PCoA), thereby using the above mentioned sample-by-trait matrix as input. Calculated indices were: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) (Villéger et al., 2008), functional dispersion (FDis; Laliberté & Legendre, 2010) and Rao's quadratic entropy (RaoQ; Botta-Dukát, 2005); see BOX 1 for definitions. Each index is an independent measure of functional trait space, and the way species are dispersed within this trait space. Apart from FRic, all indices take into account species abundance in the quantification of functional diversity, i.e. by weighting the pair-wise species dissimilarity in the trait space by the product of relative abundances of the species. This gives a differential weight to the traits of more dominant vs less abundant species, as species abundance is affecting various components of ecosystem functioning (Petchey & Gaston, 2006). A minimum of three species is needed to calculate FRic, FEve and FDiv, while FDis and RaoQ only need two.

To test for an effect of the different human activities on the FD indices, linear mixed-effect models (lmer, from the 'lme4′ package in R, Bates et al., 2014) were calculated. Four impact categories (*none, low, medium, high*) were defined for the sand extraction and dredge disposal cases, based on extracted volumes 365 days prior to sampling or yearly disposed volumes respectively (Table 1). Fixed terms in our analyses then included these categories, next to 'habitat' (levels: *Abra alba*, *Macoma balthica*, *Nephtys cirrosa*) in the dredging case and 'extraction area' (levels: *BR, HB, TB*) in the sand extraction case. Cut-off values were chosen as to distribute the sites as evenly as possible over the impact categories not equal to 0. For the OWF case, a pressure covariate 'site', which allocates the sampling sites to either *impact* or *control*, and 'wind farm' (either *Belwind* or *C-Power*), are used as categorical fixed factors. For each case, 'year' and 'sampling site' were incorporated as random factors, as we are not interested in differences between years of sampling but want to capture the yearly (natural) variation in our model. The fixed effects were first fitted as an interaction, which was subsequently removed if not significant. An ANOVA was then performed on the models to obtain p-values (from the 'car' package in R Fox & Weisberg (2019)), and post-hoc tests were executed with 'emmeans' to define where significant effects were situated. The residuals of the optimal models were checked for homoscedasticity, and normality of residuals evaluated using Q-Q plots, after which an x^2 or x^3 transformation was applied in the case of left-tails. Throughout the text, averages are given together with their standard deviation (SD).

2.3.3. Fuzzy correspondence analyses

To identify shifts in trait composition due to the human activities, Fuzzy Correspondence analyses (FCA) were performed with R package Ade4, using the dudi.fca function (Dray & Dufour, 2007). The input is again the sample-by-traits matrix, where the FCA analysis returns the ordination scores of traits and samples on the first two ordination axes. As such, ordination biplots can be made whereby points represent the abundance-weighted trait composition of samples, and the trait modalities that respond to the pressure (response traits) or which are associated with the shift but are not directly responding to the pressure (effect traits) are plotted as well. Points in closer proximity are indicative of samples with a functional similarity. The dredging pressure categories ('none', 'low', 'medium' and 'high'), related to dredge disposal and sand extraction volumes, and the control/impact sites for the OWF case, were then superimposed on the reduced two-dimensional ordination output and the pairwise distances between the centroids were calculated and used as a proxy for the relative similarity between those groups (cfr. Bolam et al., 2016). The FCA analysis was performed separately for each concession/extraction area in the case of resp. wind energy exploitation and sand extraction and per habitat type in the case of dredge disposal. These analyses were done based on all traits together and also based on response and effect traits separately. Where the impact regimes are separated on the first or second axis without too much overlap, the arrangement of the traits on that FCA axis was extrapolated and placed on a gradient ranging from impact to control, this way traits associated with the impact samples could be identified. All statistical analyses and data visualizations were performed using the R software (R Core Team, 2020).

3. Results

3.1. Functional diversity indices

3.1.1. Dredge disposal

There was a significant interaction effect for FRic, FEve and RaoQ (intensity × habitat, resp. $p < .00001$, $p < .05$ and $p < .05$; Annex Table A3). For the *Nephtys cirrosa* habitat, no significant differences between the different dredge disposal levels were observed (all $p > .05$) (Fig. 2). In *Abra alba* habitat, FRic was significantly lower at 'medium' (26 ± 13) and 'high' (28 ± 11) levels of dredge disposal compared to 'low' (45 ± 6) and 'none' (41 ± 9), while FEve was significantly higher at 'medium' (0.69 ± 0.12) levels of dredge disposal compared to 'low' (0.61 ± 0.09) and 'none' (0.59 ± 0.10). RaoQ was significantly lower at 'medium' (26 ± 8) and 'high' (25 ± 9) levels of dredge disposal compared to 'low' (37 ± 7), and also significantly lower at 'high' levels compared to 'none' (32 ± 9). In *Macoma balthica* habitat, FRic was significantly lower at 'medium' (15 ± 9) and 'high' (13 ± 7) dredge disposal levels compared to 'low' levels (28 ± 12), and FEve was significantly higher in samples that received 'high' (0.71 ± 0.20) levels of dredge disposal compared to 'low' (0.61 ± 0.12) and 'none' (0.58 ± 0.17), while RaoQ was the other way around, with lower values at 'high' (18 ± 11) versus 'low' (28 ± 8) levels of dredge disposal. FDiv and FDis followed the same trends across all three habitats (intensity × habitat, all $p > .05$*)* but differed significantly between habitats (habitat: resp. $p < .05$ and $p < .00001$). FDis was significantly higher in *Abra alba* habitat (5.1 ± 1.1) compared to *Macoma balthica* (4.3 ± 1.5) and *Nephtys cirrosa* habitat (4.1 ± 1.4). For FDiv, values were higher in *Abra alba* (0.76 ± 0.13) compared to *Macoma balthica* (0.73 ± 0.15) habitat. FDis was also significantly differed between intensity levels ($p < .0001$) with significantly lower values at 'high' (4.1 ± 1.6) levels of dredge disposal compared to 'medium' (4.5 ± 1.3), 'low' (4.8 ± 1.1) and 'none' (4.6 ± 1.4). A table containing the p-values of all main and pairwise tests is found in Annex Table A3.

Table 1
Number of samples allocated to each category, grouped by benthic habitat type and by sand extraction zone.

	None	Low	Medium	High
DREDGE DISPOSAL	*0*	*1-2e⁶ tons/disposal site/year*	*2e⁶-4e⁶ tons/disposal site/year*	*4e⁶-10e⁶ tons/disposal site/year*
Abra alba	114	40	22	77
Macoma balthica	144	49	49	13
Nephtys cirrosa	66	28	35	0
SAND EXTRACTION	0	1–200 m^3/7800 m^2/year	200–2000 m^3/7800 m^2/year	2000–20000 m^3/7800 m^2/year
Buiten Ratel	136	21	25	27
Hinderbanken	64	5	15	9
Thorntonbank	70	30	22	5

BOX 1

Functional diversity indices – definitions and conceptual diagrams (based on Villéger et al., 2008 and Laliberté & Legendre, 2010).

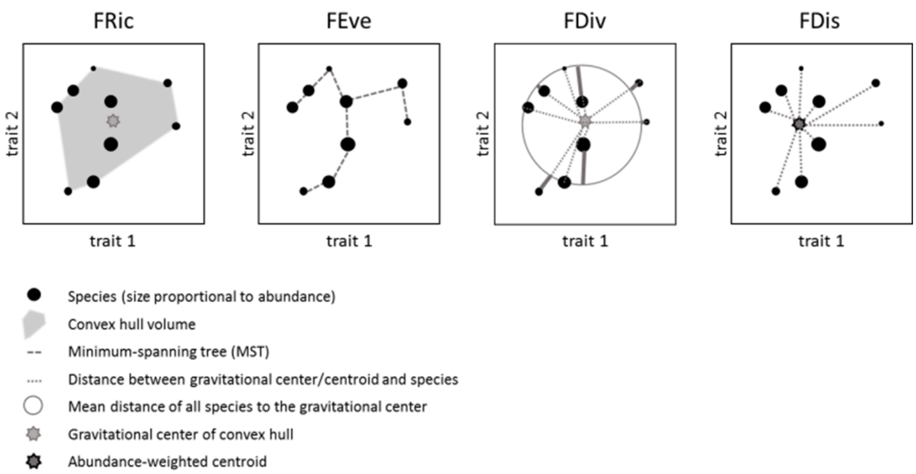
FRic: functional richness represents the total amount of functional space filled by the community (minimum convex hull volume) and has no upper limit.

FEve: functional evenness represents the evenness of species abundance distributions in functional trait space (average branch length of minimum-spanning tree, weighted by relative abundance), and ranges between 0 and 1.

FDiv: functional divergence measures distribution within trait space (individual species' deviation from the mean distance of all species to the gravitational center of the convex hull) and ranges between 0 and 1.

FDis: functional dispersion measures distribution within trait space (mean distance of each species to the abundance-weighted centroid of the community and has no upper limit.

RaoQ: Rao's quadratic entropy is a generalized form of the Simpson index, which measures the amount of trait dissimilarity between two random individuals in the community (conceptually similar to FDis but more widely used in marine impact assessment research), and has no upper limit.



Graphs designed after Villéger et al. (2008) and Laliberté et al. (2010).

3.1.2. Sand extraction

No significant differences were detected for any of the extraction zones at different levels of sand extraction for FDiv (Annex Table A4, all p >.05), which centered around 0.75 (Fig. 2). FRic had no significant interaction effect, only a small significant effect of area, with higher values at Buiten Ratel (36 ± 11) compared to Hinderbanken (31 ± 10). FEve, FDis and RaoQ all had significant interaction effects (Table A4, resp. p <.0001, p <.001 and p <.001). At Buiten Ratel, FEve was significantly higher at 'high' levels of extraction (0.68 ± 0.08) compared to 'medium' (0.59 ± 0.0.9) and 'none' (0.61 ± 0.09), while at Hinderbanken, it was significantly lower at 'high' levels of extraction (0.56 ± 0.08) compared to 'medium' (0.70 ± 0.08) and 'none' (0.66 ± 0.09). FDis and RaoQ were significantly higher at 'high' levels (resp. 6.0 ± 0.8 and 39 ± 9) compared to 'medium' (resp. 5.1 ± 0.8 and 30 ± 10), 'low' (resp. 4.6 ± 1.4 and 26 ± 11) and 'none' (resp. 5.1 ± 0.8 and 30 ± 9) at Buiten Ratel only. At Thorntonbank, none of the functional diversity indices yielded a significant difference. A table containing the p-values of all main and pairwise tests is found in Annex Table A4.

3.1.3. Wind farms

FRic yielded a significant response to the impact of turbines, but only in C-Power (wind farm × site: p <.01), with a higher average value at IMP sites (26 ± 13) compared to the control sites (20 ± 10) (Fig. 2). For the other functional diversity induces under study, differences between OWFs appeared to be more pronounced than differences within each OWF between impact levels, as FEve, FDis and RaoQ only had a significant effect of wind farm (resp. p <.0001, p <.05, p <.0005, and p <.001). They were significantly higher at Belwind (resp. 0.7 ± 0.1; 5.3 ± 0.1 and 32 ± 10) compared to C-Power (resp. 0.6 ± 0.2; 4.6 ± 1.2 and 26 ± 10), while FDiv showed higher values at the C-Power OWF (resp. 0.81 ± 0.10 and 0.85 ± 0.10). A table containing the p-values of all main and pairwise tests can be found in Annex Table A5.

3.2. Fuzzy correspondence analyses (FCA)

3.2.1. Dredge disposal

For the *Abra alba* habitat analysis using all traits, the two first principal axes account for only 30.6 % of the total amount of inertia (resp. 18 and 12.6 %). There is a visual separation on the second ordination axis as 'none' and 'low' appear below 'medium' and 'high' (Fig. 3). This is also shown by the pair-wise distances in Table 3, as this distance is in most cases higher between the extreme impact categories (e.g. 'low'-'high'). The trait modality associated most with the higher disposal pressures is egg development asexual (edAsex) and Sexual benthic (Fig. 3). The trait shifts are greater when the ordination is based on effect traits (Table 2 and Annex A6a). For the *Macoma balthica* habitat analysis using all traits, both first ordination axes account for 37.9 % of the total amount of inertia (resp. 21.2 and 16.7 %). It is clear from Fig. 2 that there is too much overlap to allocate a disposal pressure gradient to either of the axes, although the pairwise distances between the centroids of the pressure categories suggest some extent of separation (Table 2). Overall, the response traits yielded a better separation between the pressure categories when comparing the pair-wise distances of the ordinations based on response or effect traits (Table 2, Annex A6b). For the *Nephtys cirrosa* habitat analysis using all traits, the first two ordination axes explain 43.8 % of the total inertia (resp. 29.4 and 14.4 %). None of the

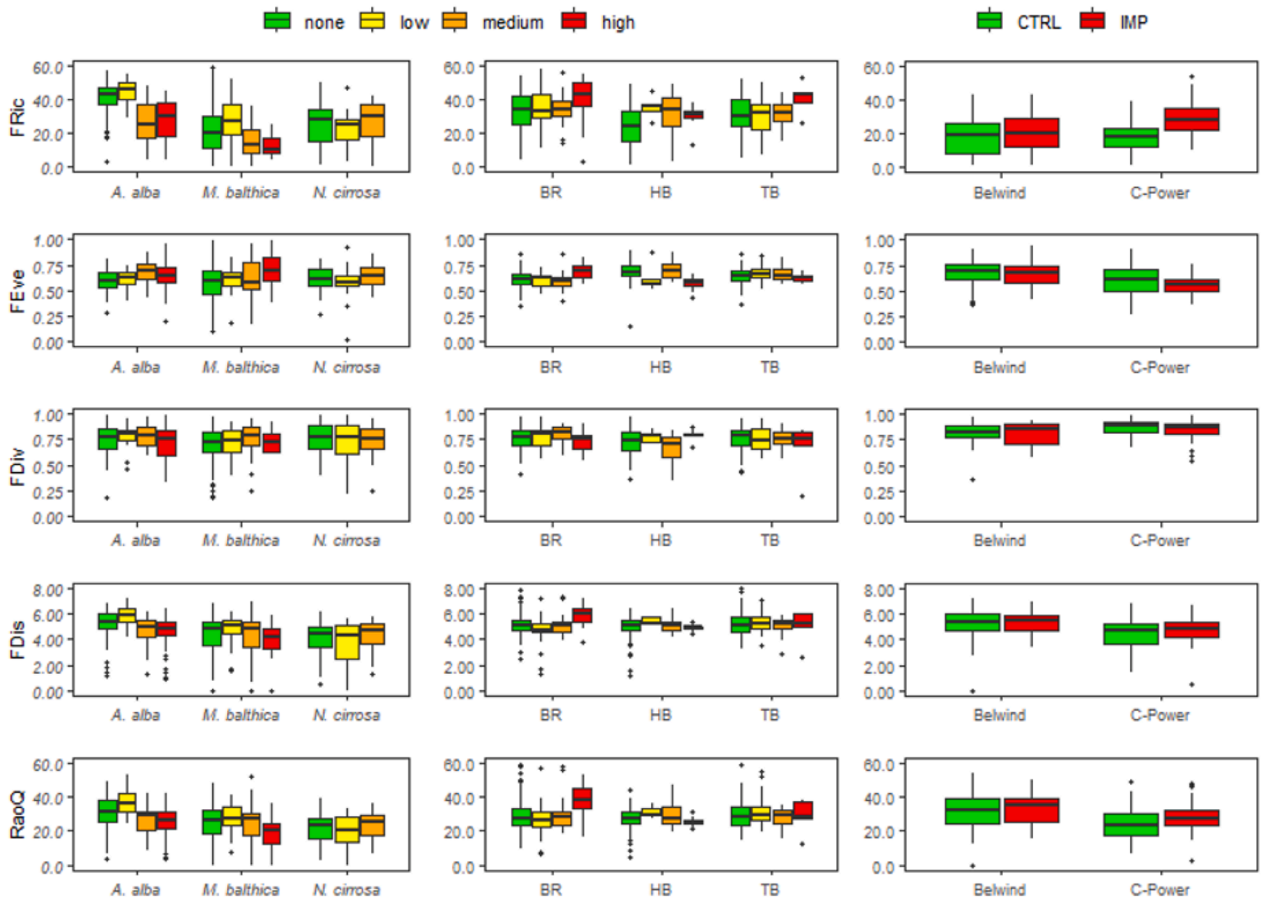


Fig. 2. Boxplots of the functional diversity indices for the three cases. The names of the sand extraction zones have been abbreviated for space limitation purposes (BR = Buiten Ratel, HB = Hinderbanken, TB = Thorntonbank).

samples experienced a 'high' disposal pressure and the centroids are located in the middle of the sample cloud, making it difficult to allocate a disposal pressure gradient. When comparing the ordinations using only the response or effect traits, the response traits yielded a better separation (Table 2 and Annex A6c).

3.2.2. Sand extraction

The first two ordination axes of the FCA plot of Buiten Ratel using all traits explain 32.3 % (resp. 20.8 and 11.5 %) of the total inertia (Fig. 4). The samples that experienced a 'high' extraction pressure are clearly separated from the other categories. The community associated with this 'high' pressure consists of individuals with an epibenthic or attached lifestyle, or that live in crevices (lhEpi, lhAttach, lhCrevice), that have an asexual egg development (edAsex) and no bioturbation activities (btNone). When comparing the pair-wise distances, the response traits yielded the best separation between 'high' and the other pressure categories (Table 2 and Annex A7a). For Hinderbanken, the first two ordination axes explain 30 % of the total interia (resp. 16.8 and 13.2 %) when using all traits. The lower pressure categories are located above'high' and 'medium, so there is a slight separation on the second axis (Fig. 4). There is a high occurrence of asexual development (edAsex) in this community, together with a parasitic feeding mode (fmPar), large body size (sr500) and no bioturbatory activity (btNone). When comparing the pairwise distances of the ordinations based on response or effect traits, the effect traits are clearly the cause of the distinction between 'high' and the lower pressure categories, as is also illustrated by Table 2 and Annex A7b. For Thorntonbank, the two first axes together explain 33.8 % of total inertia (resp. 20.2 and 13.6 %) when using all traits. The 'high' pressure category is clearly separated from the other categories on the second ordination axis, which is also the case on the ordinations using only response or effect traits (Annex A7c), and this separation is the greatest using only effect traits (Table 2). The community associated with this 'high' pressure consists of large (sr201-500), bioturbators (bdDown, btUp), animalswith an epiphytic lifestyle (lhEpi), asexual egg development (edAsex) and parasitic feeding mode (fmPar).

3.2.3. Wind farms

The impact and control samples are well separated on both the first and second FCA axis, which together account for 39.9 % (Belwind) and 37.2 % (C-Power) of the explained inertia (Fig. 5). This distance is a bit larger for C-Power at Thorntonbank compared to Belwind at Bligh Bank (resp. 2.8 and 1.8). The impact and control samples of Thorntonbank are separated more along the first ordination axis, while Belwind is more clearly divided on the second axis. Parasites and organisms with no bioturbatory activity (fmPar, btNone) are found in greater numbers both in the impact samples of C-Power and in the control samples of Belwind. C-Power also has more individuals with an attached and epiphytic lifestyle (lhEpi, lhAttach) occurring in its impact samples. The separation between control and impact samples is larger when using only response traits in the case of C-Power, and when using only effect traits in the case of Belwind (Table 2).

4. Discussion

In this study, the applicability of functional diversity indices and fuzzy correspondence analyses in assessing the consequences of human activities on benthic functional properties is investigated. The applicability was demonstrated for three human activities: dredge disposal,

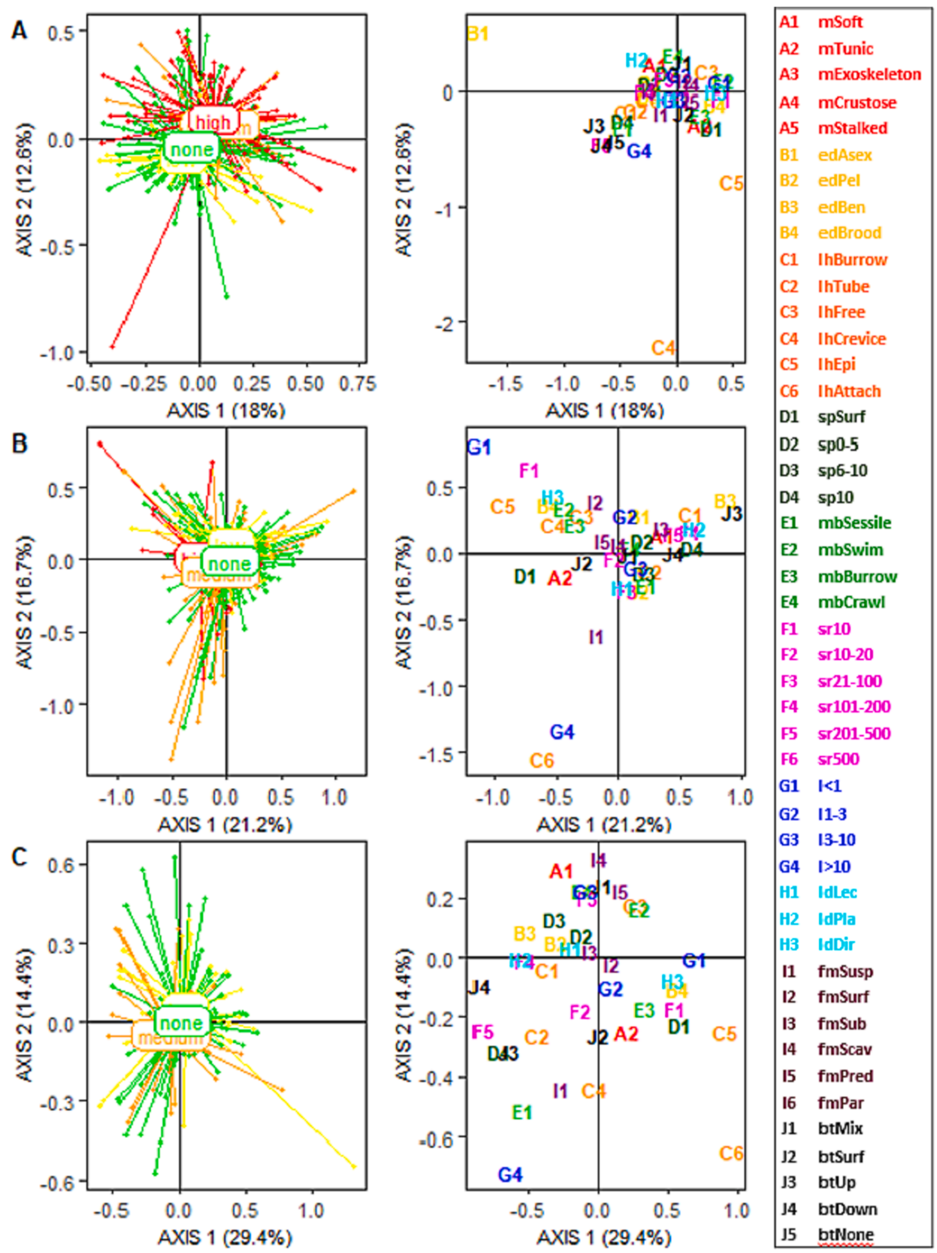


Fig. 3. FCA ordination plots for the dredge disposal case (A = *Abra alba* habitat, B = *Macoma balthica* habitat, C = *Nephtys cirrosa* habitat), the samples are plotted on the left and colored according to their pressure categories (none - green, low - yellow, medium - orange, high – red), the trait modalities are plotted on the graphs on the right. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sand extraction and offshore wind energy exploitation. In general, it shows that responses are complex, and depend strongly on both the degree of impact and the habitat characteristics of the sites (Table 3). The outcomes of this study are setting the scene of including BTA analyses in environmental impact analyses, but more detailed (experimental) studies are needed to effectively unravel the effects on ecosystem functioning.

4.1. *The responses are complex and habitat-dependent*

4.1.1. *Habitat dependency*

The habitat dependency of the response of functional indices to disturbance was tested for the dredge disposal sites, as they are located in three different habitats (*A. alba, M. balthica and N. cirrosa*). The three indices that showed a significant response to dredging (FRic, FDis, RaoQ) had significantly higher values in *A. alba* habitat compared to the other two. This is in accordance with the findings of Breine et al. (2018), where this fine muddy sand habitat exhibited the highest densities, species richness and structural and functional diversity. The decline of functional richness in the samples that experience high dredge disposal intensity seems to be a result of the loss of species that cannot cope with the higher disturbance, On the other hand, the *N. cirrosa* habitat, originally consisting of sandy sediments (Breine et al., 2018), gets enriched with organic material because of disposal of muddy sediments and thereby attracts new opportunistic species (Van Hoey et al., 2022). The increased structural diversity is not reflected in the addition of new trait modalities (no response of the functional diversity indices) and also the FCA show no clear shift in the pressure categories. This is linked to the fact that the traits of the new species are similar than the baseline sandy community, dominated by smaller, shorter living species (Breine et al., 2018). In *M. balthica* habitat, the pressure categories could also not be discerned in the FCA plot. This could be related to the natural

Table 2
Pair-wise distances of group regime centroids. When comparing the distances using response or effect traits, the highest values are put in bold.

		Dredge disposal									Sand extraction								
		A.alba			*L. balthica*			*N. cirrosa*			BR			HB			TB		
		All	Resp	Eff	All	Resp	Eff	All	Resp	Eff	All	Resp	Eff	All	Resp	Eff	All	Resp	Eff
NONE	LOW	0.7	0.5	**0.9**	1.2	0.8	**1.4**	0.5	0.5	**0.6**	0.8	**0.8**	0.5	1.6	1.2	**2.2**	0.6	**0.8**	0.6
	MEDIUM	1.7	1.2	**1.6**	1.2	**1.7**	1.1	1.0	**1.5**	0.7	0.4	0.4	**0.6**	1.2	**1.8**	0.9	0.7	**1.3**	0.3
	HIGH	1.7	0.9	**1.3**	2.8	**2.9**	2.8				1.3	**1.3**	0.8	1.1	1.6	1.6	2.2	0.7	**3.3**
LOW	MEDIUM	2.3	1.6	**2.4**	2.2	**2.5**	1.5	1.5	**1.7**	1.2	0.3	0.3	0.5	2.2	1.4	**2.8**	0.4	0.6	**0.8**
	HIGH	2.3	1.4	**2.1**	3.1	**3.2**	3.0				1.1	**1.1**	0.4	1.6	0.6	**2.4**	2.0	1.4	**3.0**
MEDIUM	HIGH	0.4	**0.4**	0.3	2.1	**2.6**	1.7				1.1	**1.1**	0.4	0.6	**1.9**	1.2	2.4	1.7	**3.3**

		OFFSHORE WIND FARMS					
		Belwind			C-Power		
		All	Resp	Eff	All	Resp	Eff
CTRL	IMP	1.8	1.5	**1.7**	2.8	**2.9**	2.5

characteristics of the *M. balthica* habitat, i.e. muddy sediment characterized by opportunistic, short-living species (Breine et al., 2018), which is similar to the disposed material, that is characterized as 'liquid muddy, sludge'. Therefore, the habitat characteristics in *M. balthica* habitat and related functional trait composition will not change substantially due to this disposal regime.

All of the sand extraction zones are originally situated in *H. elongata* habitat (Breine et al., 2018). Although some of the most impacted zones (e.g. Buiten Ratel) have transitioned into a heterogenous habitat that is a mixture of sandy *H.* and more muddy *A. alba* (De Backer et al., 2014a). The increase of functional index values of samples undergoing higher sand extraction seems to indicate that the change towards the habitat type *A. alba* with a concomitant increase of new species (Wyns et al., 2021), with additional trait modalities (e.g. asexual egg development and no bioturbatory capacity).

There are no similarities in trait modalities occurring at the impact samples of both wind farms, with for instance individuals with a parasitic feeding mode and no bioturbatory capacity (fmPar, btNone) dominating both the impact samples of C-Power and control samples of Belwind.

4.1.2. Degree of impact

In theory, a decrease of taxonomic diversity corresponds to loss in functional richness, but this is not necessarily the case for the other functional indices (Gaglio et al., 2021). A loss in species richness does not imply an uneven distribution of functional attributes, a dimension computed in both functional evenness (FEve) and Rao's quadratic entropy (RaoQ) indices. These different patterns in functional indices in relation to the structural changes and the impact type is clearly reflected in the sand extraction and disposal activity cases. Sand extraction causes sediment plumes in the water column due to overflow and at the seabed due to physical disturbance of the draghead (Tillin et al., 2006). Dredge disposal activities mainly cause changes in the habitat due to smothering by the disposed material (Bolam et al., 2006). In our study area, these different impacts resulted in a similar structural change, i.e. a local biodiversity increase, in the macrobenthic assemblages (De Backer et al. 2014b), while our study reveals that functional diversity indices depict different responses.

An increased sand extraction pressure mostly leads to higher values of nearly all indices (except for FDiv and at Hinderbanken, where functional evenness was significantly lower at higher pressure), whereas a higher amount of dredge disposal leads to significantly lower index values for functional richness, functional dispersion and Rao's quadratic entropy (Table 3). Functional evenness however increases with higher disposal pressure, which means that the functional modalities are then present in equal proportions in the disposal areas. The difference in FEve results for the different sand extraction zones, i.e. an increase of evenness at high pressure at BR and a decrease at Hinderbanken, is linked to difference in degree of impact (the duration and timing of the pressure) (Wyns et al., 2021), since Buiten Ratel was continuously exploited, while Hinderbanken only a few months per year. This periodicity leads to the recovery of some species, which could lead to dominance of certain trait-modalities, which seems not or less the case under continuous exploitation. This difference in degree of impact at both sites leads to changes in the sedimentology, the Hinderbanken is evolving into *N. cirrosa* community (naturally lower diversity values) and Buiten Ratel into *A. alba* community (naturally higher diversity values) (Breine et al., 2018). The presence of wind farms only led to a significantly higher functional richness in one of the offshore wind farms and differences between OWFs appears to be more pronounced than the differences related to the actual human activities (impact vs control) within parks. However, at C-Power, functional richness was found to be higher nearby the jacket foundations compared to the control samples situated further away. Reasons for the lack of clear impact-related effects at nearby distances within Belwind is related to the fact that the environmental conditions are different, which are stronger bottom currents and less divers and abundant benthic community compared to C-power area. The extent of the artificial reef effect is depending on the site specific conditions (depth, hydrodynamic regime) and turbine-associated technical differences (shape, size, density) (Lefaible et al., 2018, Lefaible et al. submitted). So, it maybe that the impacts related to the "artificial reef" are only detectable at closer distances from the monopiles within the Belwind OWF.

Functional correspondence analysis is giving similar and some complementary information to the patterns revealed by the functional diversity indices. As such, this technique allows to focus more on the traits themselves, which are possibly shifted due to the pressure caused by the different human activities. In general, there seem to be no similar disturbance-induced functional responses in the traits across the activities (Table 3). With the exception of the dredge disposal case in *M. balthica* and *N. cirrosa* habitat, the centroids of the pressure categories on the FCA plot were separated to some visible extent and these shifts could be linked to some frequently occurring trait modalities. Nevertheless, a contradictory observation was also made, as some communities experiencing high extraction pressure have higher frequencies of large individuals (Thorntonbank & Hinderbanken, respectively sr201-500 & sr500), while these exact traits were assessed to be sensitive to the effects of sediment abrasion caused by sand extraction (Kenny et al., 2018). The species found can potentially grow very large (trait categorization), but this is not necessarily the case for the individuals which are present, as these species can persist in the community as smaller individuals, that will not reach old age. The 'high' impact zones of all sand extraction sites on the other hand have a higher frequency of asexual development.

In general, Mouillot et al. (2013) showed that all functional diversity indices were expected to decrease after disturbance. As this is not true in

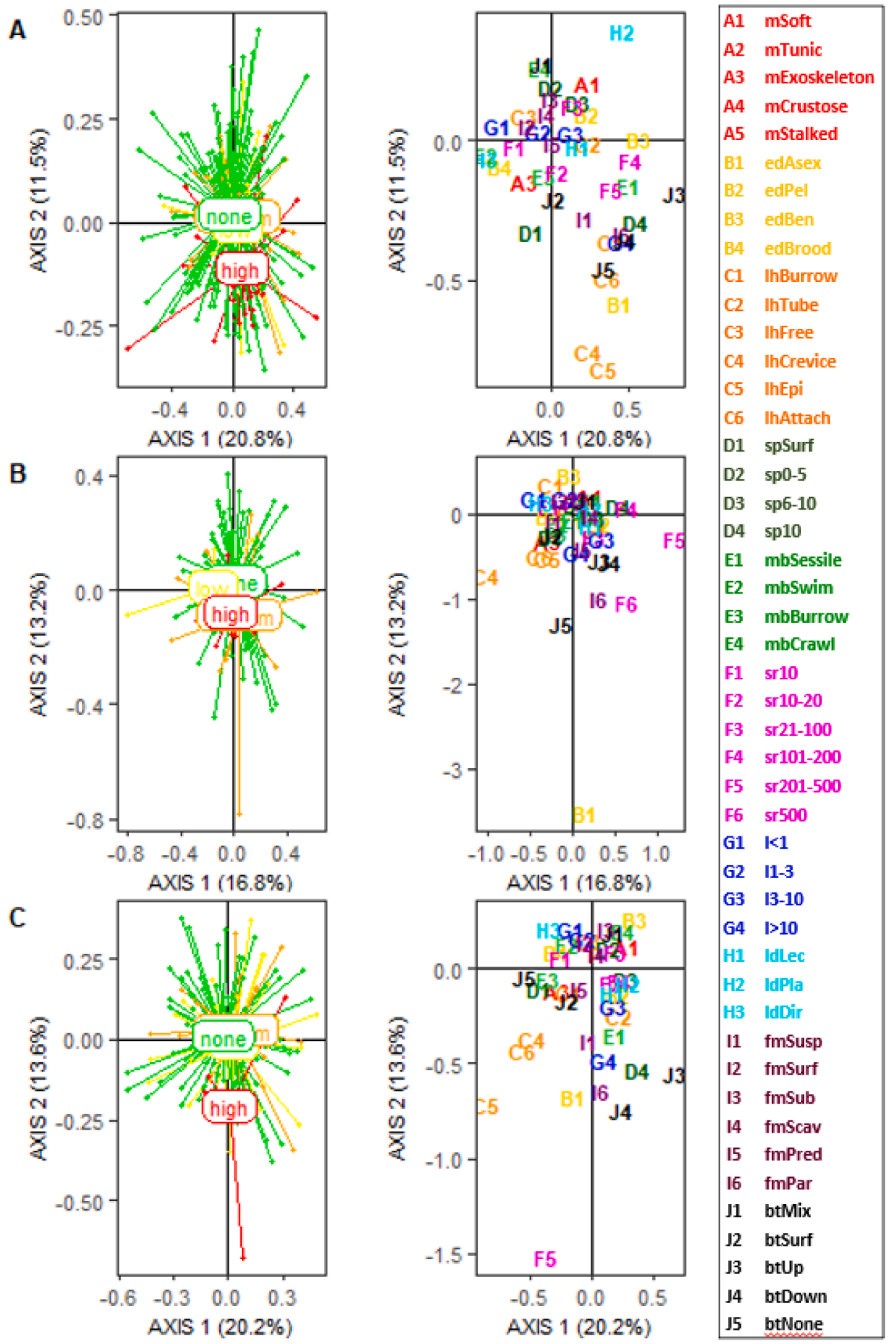


Fig. 4. FCA ordination plots for the sand extraction case (A = Buiten Ratel, B = Hinderbanken, C = Thorntonbank), the samples are plotted on the left and colored according to their pressure categories (none - green, low - yellow, medium - orange, high – red), the trait modalities are plotted on the graphs on the right. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

our case studies, a possible explanation is that the BPNS has been intensively exploited for decades, and benthic communities are known to be less sensitive to local-scale impacts in areas with already high natural physical disturbance (Cooper et al., 2011). Indeed, significant differences are mainly found when comparing the 'high' pressure category with the controls (category 'none'). This indicates that the benthic communities of the BPNS can cope with a rather high level of pressure before significant changes in functional biodiversity are found.

4.1.3. *Functional responses when considering effect – response traits*

As per example of Bolam et al. (2016), the ten chosen biological traits were compartmentalized into response and effect traits, to potentially understand why a community shift develops under certain pressures, and how this in turn affects the ecosystem. This was done by producing FCA plots separately for response and effect traits and comparing the distances between the pressure category centroids, with larger distances indicating that those sets of traits were more heavily influenced. The results on effect – response traits also show a mixed pattern among pressure type and habitat, as outlined above. Sand extraction seems to influence effect traits more, as the distance between the centroids of none and high impact are located further away when only considering those traits in 2 of the three extraction zones, while dredge disposal predominantly affects response traits (*N. cirrosa* & *M. balthica* habitat). At the OWFs, pairwise distances between control and impact centroids

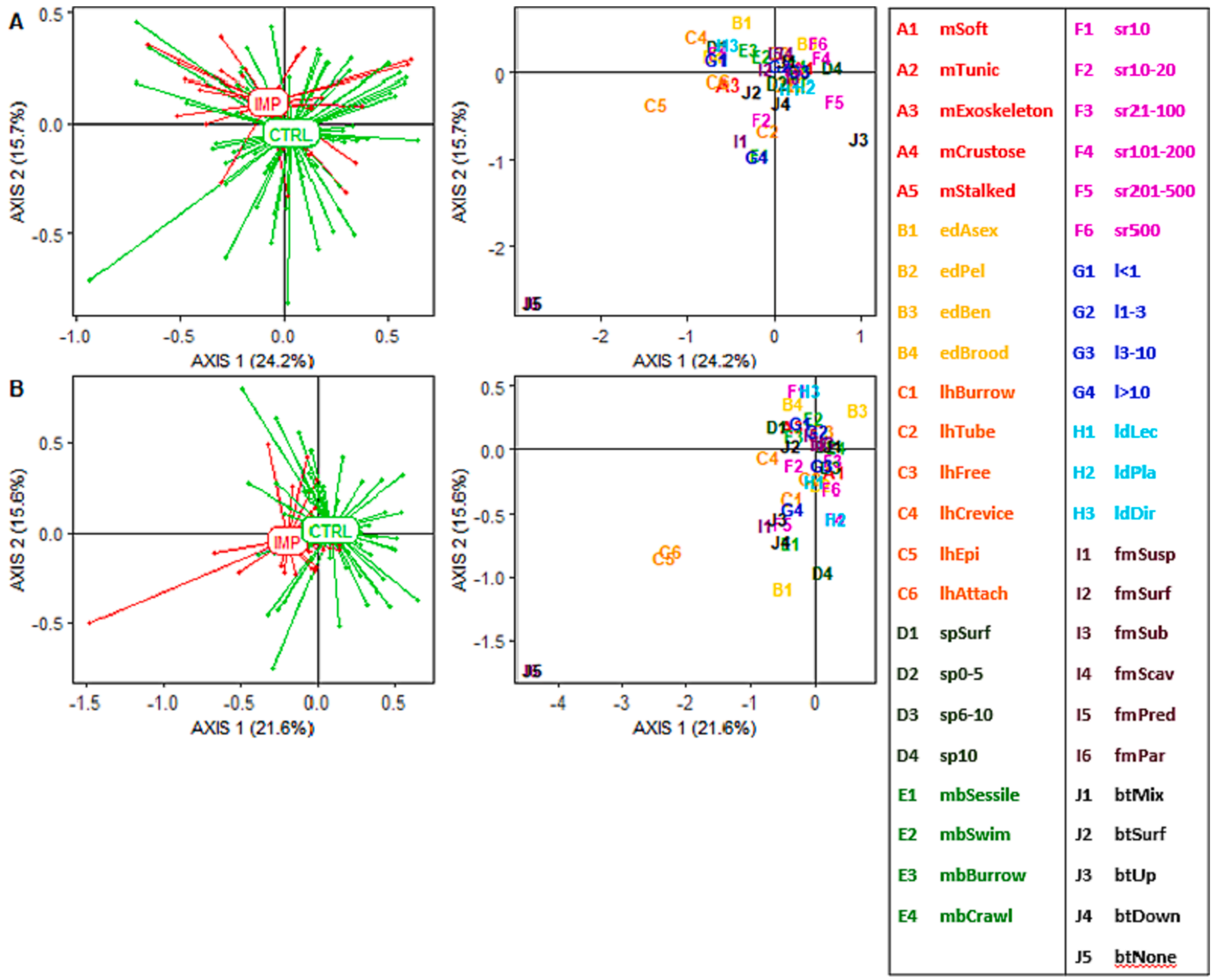


Fig. 5. FCA ordination plots for the offshore wind farm case (A = Belwind, B = C-Power), the samples are plotted on the left and colored according to their pressure categories (none - green, low - yellow, medium - orange, high – red), the trait modalities are plotted on the graphs on the right. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Summary table representing the observed changes in the three cases studies for the univariate (functional diversity indices) and multivariate (FCA analyses) analyses, using all traits. '+' indicates an increase, '-' indicates a decrease and '0' indicates no significant change at (higher) impact.

		FRic	FEve	FDiv	FDis	RaoQ	FCA (separation)	Effect/response traits determine difference between none-high impact (based on Table II)	Indicative trait modalities occurring at the extreme axis positions
Dredge disposal	*A. alba*	−	+	0	−	−	yes	effect	edAsex, edBen,lhCrevice, lhepi
	M. balthica	−	+	0	−	−	no	response	/
	N. cirrosa	0	0	0	−	−	no	response	/
Sand extraction	Buiten Ratel	0/+	+	0	+	+	yes	response	lhEpi, lhCrevice, edAsex, lhAttach, btNone
	Hinderbanken	0/+	−	0	0	0	yes	effect	edAsex, fmPar, sr500, btNone
	Thorntonbank	0/+	0	0	0	0	yes	effect	sr201-500, btDown, lhEpi, edAsex, fmPar
OWF	C-Power	+	0	0	0	0	yes	response	bNone, fmPar, lhEpi, lhAttach
	Belwind	0	0	0	0	0	yes	effect	Sr500, edBen, lhCrevice, edAsex

only slightly differ, whether the analysis is performed on response or effect traits. No obvious reason for those different response-effect trait patterns across the cases. Combined with the fact that the traits shifts are not strongly pronounced between the pressure categories, more in depth research is needed to unravel possible mechanistic responses. Based on overarching analyses, as done in this study, no defined conclusion can be made.,

4.2. Applicability

4.2.1. Traits

Biological trait analyses (BTA) necessarily rely on expert knowledge and the simplification of biological trait information by the categorization of traits. As a consequence, some considerations have to be made. First, the resulting species-traits tables used to calculate indices and perform analyses such as FCA are usually not shared among many different BTA studies, which makes it hard to compare outcomes. Nowadays, there exists a wide set of trait databases (de Juan et al., 2022; Martini et al., 2021; Smit et al., 2021) and some studies (Hewitt et al., 2011; Thrush et al., 2017) could not detect significant effects of different expert knowledge on the end results of BTA studies. Second, functional indices and FCA are highly sensitive to trait measure errors (Pakeman, 2011; Lefcheck et al., 2015), meaning that biological/functional traits using literature data may introduce some errors and omit the capacity of ecological plasticity of some taxa and therefore hiding the true variability within the dataset (de Juan et al., 2022). Therefore, the pressure impacts on traits diversity and trait shifts we observed here are interpreted with care, and the observations are based on a large spatial–temporal dataset of a well-known area. Third, trait modalities are reflecting the species trait potential, as for example for maximum size and lifespan, which are mostly not reached for the individuals within the data. This could give a distorted image if for instance large, long-living species are depicted on the FCA in highly disturbed habitat (e.g. Buiten Ratel in our study). Fourth, certain trait modalities seem present in the study area where this is not necessarily the case. This is related to higher taxa level determinations, wherefore the fuzzy coding spread the scores across all modalities within a trait. This was for example the case in this study for the high occurrence of parasitic feeding mode (fmPar) in the impact samples of Hinderbanken and Thorntonbank, attributed to the presence of Gastropoda juveniles. Despite some points of consideration related to traits classifications, it is a standard, well-known methodology, which provides a rapid methodology to get insights on changes in benthic functional properties due to different pressures and can supplement taxonomic analysis, as shown in this study.

4.2.2. Functional diversity indices

As functional diversity includes different components (richness, evenness and divergence) taking into account trait values and their abundance, the functional diversity cannot be summarized by a single number (Villéger et al., 2008). Therefore, it is advisable to consider the entire set of functional diversity indices to evaluate changes in the benthic ecosystem due to anthropogenic activities. On the other hand, some indices can be more responsive or reliable in certain cases (e.g. FDiv and RaoQ in the case of sewage pollution (Leite Gusmao Junior, 2017). Nevertheless, FDiv was not responsive in our three cases as it yielded approximately the same mean value. This makes sense however, since trait divergence is expected to arise from strong competitive interactions (Peronne et al., 2017), which are generally thought to be rather weak in soft-bottom environments (Defeo & McLachlan, 2005; Wilson, 1991). FRich was the most responsive index in our study, with differential outcomes in response to sand extraction and dredge disposal, and the only index that yielded a significant difference between impact and control sites at the C-Power wind farm. The index does not respond to changes in the relative proportion of species and thus can be highly sensitive to functionally unique “outliers” that may be present at low abundances (Laliberté & Legendre, 2010; Villéger et al., 2008). Feve increased in most of our cases, which was not expected as this indicates lower niche overlap and better resource utilization at higher pressure. FRich and Feve both can be interpreted as indicators for productivity, buffering against environmental fluctuations, or vulnerability to invasion (Mason et al., 2005). Fdis has shown to be significantly correlated with Rao’s quadratic entropy (van der Linden et al., 2016), which is to be expected as they have a similar mathematical background (Laliberté & Legendre, 2010; Mason et al., 2013). This was also clear from our results, which proves that they are redundant and only one of them should be included in further research. As Rao’s quadratic entropy is more widespread in ecological research, we advise to opt for this one. We conclude that in dynamic soft sediments FRic and RaoQ seem to be appropriate functional indices to evaluate the impact of human activities on the functional diversity of the sea-bottom ecosystem.

4.2.3. FCA

Functional correspondence analysis (FCA) can be very useful to explore how/why assemblages respond to a pressure, which traits respond to which pressures, and the potential functional consequences of the difference pressures (Bolam et al., 2021). Nevertheless, the use of FCA as indicator approach seems currently less appropriate, due to the fact that FCA are relative ordinations, which reduce the possibility to compare analyses, and that a quantitative parameter suited for indicator-based assessments cannot be derived. A derived parameter from the FCA that we used is the centroid distances between the factors (e.g. impact categories), but these values cannot be mathematically compared between analyses. This can possibly evolve when further specific FCA statistics are being developed. Despite this shortcoming, FCA is a very useful tool to visualize shifts in traits composition between control and different impact categories and it delivers insights in the functional traits more or less associated with the impact gradient. Nevertheless, our analyses and the literature confirm that there are no traits or trait-modalities that were consequently more associated to certain pressure impacts. The response is again dependent on the habitat and the pressure gradient.

4.2.4. Conclusion on applicability in environmental impact assessments (EIA)

The context-dependent responses of BTA in this study stress the necessity to evaluate effects of human activities per habitat and impact type in environmental impact assessments. Therefore, it is not (yet) possible to generalize observed local patterns for sand extraction, dredge disposal and OWF activities to other areas. This means that a type of continuous monitoring and evaluation remains necessary. To facilitate comparison between this and future studies, it would be optimal if the choice of traits and indices are preserved. For EIA purpose, functional diversity indices (FRic and RaoQ) were good indices to quantify the shifts in functional properties within a benthic community due to various human activities. FCA is mainly a tool to explore functional patterns, as it is not yet possible to do quantitative comparisons to determine differences in impact degree between FCA outputs.

CRediT authorship contribution statement

Felien Festjens: Conceptualization, Data curation, Formal analysis, Methodology, Writing - original draft, Writing - review & editing. **Jolien Buyse:** Formal analysis. **Annelies De Backer:** Writing - original draft, Writing - review & editing. **Kris Hostens:** Writing - original draft, Writing - review & editing. **Nene Lefaible:** Writing - original draft, Writing - review & editing. **Jan Vanaverbeke:** Writing - original draft. **Gert Van Hoey:** Conceptualization, Funding acquisition, Methodology, Supervision, Writing - original draft, Writing - review & editing.

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.

Data availability

Data will be made available on request.

Acknowledgments

This study was executed within the framework of several projects: the Face-it project (BR/154/A1/FaCE-It: Functional biodiversity in a Changing sedimentary Environment: Implications for biogeochemistry and food webs in a managerial setting); Bagger project (Biological and chemical ecosystem monitoring at the dredge disposal sites financed by Flemish Authorities, Flanders Maritime Access Division); Zand (Financial support was provide by the continuous monitoring program ZAGRI, paid from the revenues of marine aggregate extraction in Belgian waters (RD 9/04/2014, Numac:2014011344) and the WinMon.BE monitoring program, OWF sample processing was carried out with infrastructure funded by EMBRC Belgium – FWO international research infrastructure IOO1621N. The data used in this study were gathered within the framework of numerous national research projects and monitoring programs executed by the Marine Biology Research Group of Ghent University and the Institute of Agricultural and Fisheries Research. We thank the crew of RV Belgica for excellent cooperation, as well as the Belgian Science Policy (Belspo) and RBINS-OD Nature for providing shiptime. Also, the crew of RV Simon Stevin and VLIZ are acknowledged for providing shiptime and for the help during sampling. Thanks as well to all research scientists, technicians and students of both institutes for their help with sorting the samples and identifying the organisms and the ILVO statistician for help with the statistical design.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.109854.

References

Andersen, K.H., Berge, T., Gonçalves, R.J., Hartvig, M., Heuschele, J., Hylander, S., Jacobsen, N.S., Lindemann, C., Martens, E.A., Neuheimer, A.B., Olsson, K., Palacz, A., Prowe, A.E.F., Sainmont, J., Traving, S.J., Visser, A.W., Wadhwa, N., Kiorboe, T., 2016. Characteristic sizes of life in the oceans, from bacteria to whales. Ann. Rev. Mar. Sci. 8, 217–241. https://doi.org/10.1146/annurev-marine-122414-034144.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting Linear Mixed-Effects Models using lme4. http://arxiv.org/abs/1406.5823.

Beauchard, O., Veríssimo, H., Queirós, A.M., Herman, P.M.J., 2017. The use of multiple biological traits in marine community ecology and its potential in ecological indicator development. Ecol. Ind. 76, 81–96. https://doi.org/10.1016/j.ecolind.2017.01.011.

Bolam, S.G., 2011. Burial survival of benthic macrofauna following deposition of simulated dredged material. Environ. Monit. Assess. 181 (1–4), 13–27. https://doi.org/10.1007/s10661-010-1809-5.

Bolam, S.G., McIlwaine, P., Garcia, C., 2021. Marine macrofaunal traits responses to dredged material disposal. Mar. Pollut. Bull. 168, 112412.

Bolam, S.G., Rees, H.L., Somerfield, P., Smith, R., Clarke, K.R., Warwick, R.M., Atkins, M., Garnacho, E., 2006. Ecological consequences of dredged material disposal in the marine environment: a holistic assessment of activities around the England and Wales coastline. Mar. Pollut. Bull. 52 (4), 415–426. https://doi.org/10.1016/j.marpolbul.2005.09.028.

Bolam, S.G., McIlwaine, P.S.O., Garcia, C., 2016. Application of biological traits to further our understanding of the impacts of dredged material disposal on benthic assemblages. Mar. Pollut. Bull. 105 (1), 180–192. https://doi.org/10.1016/j.marpolbul.2016.02.031.

Botta-Dukát, Z., 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. J. Veg. Sci. 16 (5), 533–540.

Breine, N., De Backer, A., Van Colen, C., Moens, T., Hostens, K., Van Hoey, G., 2018. Structural and functional diversity of soft-bottom macrobenthic communities in the Southern North Sea. Estuar. Coast. Shelf Sci. 214, 173–184. https://doi.org/10.1016/j.ecss.2018.09.012.

Bremner, J., Rogers, S.I., Frid, CLJ, 2003. Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. Mar. Ecol. Prog. Ser. 254, 11–25.

Bremner, J., Rogers, S.I., Frid, C.L.J., 2006a. Matching biological traits to environmental conditions in marine benthic ecosystems. J. Mar. Syst. 60 (3–4), 302–316. https://doi.org/10.1016/j.jmarsys.2006.02.004.

Bremner, J., Rogers, S.I., Frid, C.L.J., 2006b. Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). Ecol. Ind. 6 (3), 609–622. https://doi.org/10.1016/j.ecolind.2005.08.026.

Chapman, P.M., 2017. Assessing and managing stressors in a changing marine environment. Mar. Pollut. Bull. 124 (2), 587–590. https://doi.org/10.1016/j.marpolbul.2016.10.039.

Chevene, Francois, Doleadec, Sylvain, Chessel, Daniel, 1994. A fuzzy coding approach for the analysis of long-term ecological data. Freshw. Biol. 31 (3), 295–309.

Clare, D.S., Bolam, S.G., McIlwaine, P.S.O., Garcia, C., Murray, J.M., Eggleton, J.D., 2022. Biological traits of marine benthic invertebrates in Northwest Europe. Sci. Data 9 (1), 339. https://doi.org/10.1038/s41597-022-01442-y.

Coates, D.A., Deschutter, Y., Vincx, M., Vanaverbeke, J., 2014. Enrichment and shifts in macrobenthic assemblages in an offshore wind farm area in the Belgian part of the North Sea. Mar. environ. res. 95, 1–12.

Cooper, K., Boyd, S., Eggleton, J., Limpenny, D., Rees, H., Vanstaen, K., 2007. Recovery of the seabed following marine aggregate dredging on the Hastings Shingle Bank off the southeast coast of England. Estuar. Coast. Shelf Sci. 75 (4), 547–558. https://doi.org/10.1016/j.ecss.2007.06.004.

Cooper, K.M., Curtis, M., Wan Hussin, W.M.R., Barrio Froján, C.R.S., Defew, E.C., Nye, V., Paterson, D.M., 2011. Implications of dredging induced changes in sediment particle size composition for the structure and function of marine benthic macrofaunal communities. Mar. Pollut. Bull. 62 (10), 2087–2094. https://doi.org/10.1016/j.marpolbul.2011.07.021.

De Backer, A., Hillewaert, H., Van Hoey, G., Wittoeck, J., & Hostens, K. (2014). Structural and functional biological assessment of aggregate dredging intensity on the Belgian part of the North Sea. In L. de Mol & H. Vandenreyken (Eds.), *"Which future for the sand extraction in the Belgian part of the North Sea?"*. (pp. 29–58).

De Backer, A., Breine, N., Hillewaert, H., Pecceu, E., Ranson, J., Van Hoey, G., Wittoeck, J., & Hostens, K. (2017). Ecological assessment of intense aggregate dredging activity on the Belgian part of the North Sea. In K. Degrendele & H. Vandenreyken (Eds.), *Belgian marine sand: a scarce resource?* (pp. 47–65).

De Backer, A., Van Hoey, G., Coates, D., Vanaverbeke, J., Hostens, K., 2014b. Similar diversity-disturbance responses to different physical impacts: Three cases of small-scale biodiversity increase in the Belgian part of the North Sea. Mar. Pollut. Bull. 84 (1–2), 251–262. https://doi.org/10.1016/j.marpolbul.2014.05.006.

de Juan, S., Bremner, J., Hewitt, J., Törnroos, A., Mangano, M.C., Thrush, S., Hinz, H., 2022. Biological traits approaches in benthic marine ecology: dead ends and new paths. Ecol. Evol. 12 (6) https://doi.org/10.1002/ece3.9001.

Defeo, O., McLachlan, A., 2005. Patterns, processes and regulatory mechanisms in sandy beach macrofauna: a multi-scale analysis. Mar. Ecol. Prog. Ser. 295, 1–20.

Degraer, S., Carey, D.A., Coolen, J.W., Hutchison, Z.L., Kerckhof, F., Rumes, B., Vanaverbeke, J., 2020. Offshore wind farm artificial reefs affect ecosystem structure and functioning. Oceanography 33 (4), 48–57.

Douvere, F., Maes, F., Vanhulle, A., Schrijvers, J., 2007. The role of marine spatial planning in sea use management: the belgian case. Mar. Policy 31 (2), 182–191. https://doi.org/10.1016/j.marpol.2006.07.003.

Dray, S., Dufour, A.-B., 2007. The ade4 package: implementing the duality diagram for ecologists. J. Stat. Softw. 22 (4). http://www.jstatsoft.org/.

Gaglio, M., Aschonitis, V., Muresan, A.N., Vincenzi, F., Castaldelli, G., Fano, E.A., 2021. Structural and functional variations of the macrobenthic community of the adige basin along the river continuum. Water 13 (4). https://doi.org/10.3390/w13040451.

Gogina, M., Darr, A., Zettler, M.L., 2014. Approach to assess consequences of hypoxia disturbance events for benthic ecosystem functioning. J. Mar. Syst. 129, 203–213. https://doi.org/10.1016/j.jmarsys.2013.06.001.

Gutt, J., 2017. Research on climate-change impact on Southern Ocean and Antarctic ecosystems after the UN Paris climate conference—"now more than ever" or "set sail to new shores"? Polar Biol. 40 (7), 1481–1492. https://doi.org/10.1007/s00300-016-2059-y.

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R., 2008. A global map of human impact on marine ecosystems. Science 319 (5865), 948–952.

Harley, C.D.G., Hughes, A.R., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L., Williams, S.L., 2006. The impacts of climate change in coastal marine systems. Ecol. Lett. 9 (2), 228–241. https://doi.org/10.1111/j.1461-0248.2005.00871.x.

Hewitt, J., Julian, K., & Bone, E. (2011). Chatham–Challenger Ocean Survey 20/20 Post-Voyage Analyses: Objective 10 – Biotic habitats and their sensitivity to physical disturbance. In *New Zealand Aquatic Environment and Biodiversity* (Vol. 81). Ministry of Fisheries.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol. Monogr. 75 (1), 3–35.

Leite Gusmao Junior, J. B. (2017). *Sediments and functional traits: Applying a functional trait approach to assess marine macrobenthic function* [Rijksuniversiteit Groningen]. http://www.rug.nl/research/portal.

Kenny, A.J., Jenkins, C., Wood, D., Bolam, S.G., Mitchell, P., Scougal, C., Judd, A., Degraer, S., 2018. Assessing cumulative human activities, pressures, and impacts on North Sea benthic habitats using a biological traits approach. ICES J. Mar. Sci. 75 (3), 1080–1092.

Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91 (1), 299–305. http://www.ecolag.univ-montp2.fr/softwarei.

Lam-Gordillo, O., Baring, R., Dittmann, S., 2020. Ecosystem functioning and functional approaches on marine macrobenthic fauna: a research synthesis towards a global consensus. Ecol. Ind. 115, 106379.

Lauwaert, B., Fettweis, M., de Witte, B., Van Hoey, G., Timmermans, S., & Hermans, L. (2019). *Vooruitgangsrapport (juni 2019) over de effecten op het mariene milieu van baggerspeciestortingen (Vergunningsperiode 01/01/2017–31/12/2021)*.

Lefaible, N., Braeckman, U., Moens, T., 2018. Effects of wind turbine foundations on surrounding macrobenthic communities. In: Degraer, S., Brabant, R., Rumes, B. (Eds.), Environmental impacts of offshore wind farms in the belgian part of the north sea: assessing and managing effect spheres of influence, pp. 57–77 www.naturalsciences.be.

Lefaible, N., Braeckman, U., Moens, T., 2019. Evaluation of turbine-related impacts on macrobenthic communities. In: Degraer, S., Brabant, R., Rumes, B., Vigin, L. (Eds.), *Environmental impacts of offshore wind farms in the Belgian part of the North Sea: Marking a decade of monitoring, research and innovation*, pp. 47–61.

Lefcheck, J.S., Byrnes, J.E., Isbell, F., Gamfeldt, L., Griffin, J.N., Eisenhauer, N., Duffy, J. E., 2015. Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. Nature communications 6 (1), 1–7.

Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129 (2), 271–280. https://doi.org/10.1007/s004420100716.

Martini, S., Larras, F., Boyé, A., Faure, E., Aberle, N., Archambault, P., Bacouillard, L., Beisner, B.E., Bittner, L., Castella, E., Danger, M., Gauthier, O., Karp-Boss, L., Lombard, F., Maps, F., Stemmann, L., Thiébaut, E., Usseglio-Polatera, P., Vogt, M., Laviale, M., Ayata, S.-D., 2021. Functional trait-based approaches as a common framework for aquatic ecologists. Limnol. Oceanogr. 66 (3), 965–994.

Mason, N.W.H., de Bello, F., Mouillot, D., Pavoine, S., Dray, S., Zobel, M., 2013. A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. J. Veg. Sci. 24 (5), 794–806.

Mason, N. W. H., Mouillot, D., Lee, W. G., Bastow Wilson Mason, J., H Mason, N. W., & Wilson, J. B. (2005). Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *OIKOS*, *111*(1), 112–118.

Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H., Bellwood, D.R., 2013. A functional approach reveals community responses to disturbances. Trends Ecol. Evol. 28 (3), 167–177. https://doi.org/10.1016/j.tree.2012.10.004.

Pakeman, R.J., 2011. Functional diversity indices reveal the impacts of land use intensification on plant community assembly. J. Ecol. 99 (5), 1143–1151. https://doi.org/10.1111/j.1365-2745.2011.01853.x.

Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9 (6), 741–758. https://doi.org/10.1111/j.1461-0248.2006.00924.x.

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Roche, M., Degrendele, K., Vandenreyken, H., & Schotte, P. (2017). Multi time and space scale monitoring of the sand extraction and its impact on the seabed by coupling EMS data and MBES measurements. In K. Degrendele & H. Vandenreyken (Eds.), *Belgian marine sand: a scarce resource?* (pp. 6–37).

Rumes, B., & Brabant, R. (2017). Offshore renewable energy development in the Belgian part of the North Sea. In S. Degraer, R. Brabant, B. Rumes, & L. Vigin (Eds.), *ENVIRONMENTAL IMPACTS OF OFFSHORE WIND FARMS IN THE BELGIAN PART OF THE NORTH SEA: A CONTINUED MOVE TOWARDS INTEGRATION AND QUANTIFICATION* (pp. 13–17).

Rumes, B., & Brabant, R. (2018). Offshore renewable energy development in the Belgian Part of the North Sea. In S. Degraer, R. Brabant, B. Rumes, & L. Vigin (Eds.), *ENVIRONMENTAL IMPACTS OF OFFSHORE WIND FARMS IN THE BELGIAN PART OF THE NORTH SEA: ASSESSING AND MANAGING EFFECT SPHERES OF INFLUENCE* (pp. 14–17).

Smit, K.P., Bernard, A.T.F., Lombard, A.T., Sink, K.J., 2021. Assessing marine ecosystem condition: a review to support indicator choice and framework development. Ecol. Ind. 121, 107148.

Statzner, B., Bêche, L.A., 2010. Can biological invertebrate traits resolve effects of multiple stressors on running water ecosystems? Freshw. Biol. 55 (SUPPL. 1), 80–119. https://doi.org/10.1111/j.1365-2427.2009.02369.x.

Thrush, S.F., Hewitt, J.E., Kraan, C., Lohrer, A.M., Pilditch, C.A., Douglas, E., 2017. Changes in the location of biodiversity– ecosystem function hot spots across the seafloor landscape with increasing sediment nutrient loading. Proc. R. Soc. B Biol. Sci. 284 (1852), 20162861.

Tillin, H.M., Hiddink, J.G., Jennings, S., Kaiser, M.J., 2006. Chronic bottom trawling alters the functionalcomposition of benthic invertebrate communitieson a sea-basin scale. Mar. Ecol. Prog. Ser. 318, 31–45.

van der Linden, P., Patrício, J., Marchini, A., Cid, N., Neto, J.M., Marques, J.C., 2012. A biological trait approach to assess the functional composition of subtidal benthic communities in an estuarine ecosystem. Ecol. Ind. 20, 121–133. https://doi.org/10.1016/j.ecolind.2012.02.004.

van der Linden, P., Borja, A., Rodríquez, J.G., Muxika, I., Galparsoro, I., Patrício, J., Veríssimo, H., Marques, J.C., 2016. Spatial and temporal response of multiple trait-based indices to natural- and anthropogenic seafloor disturbance (effluents). Ecol. Ind. 69, 617–628. https://doi.org/10.1016/j.ecolind.2016.05.020.

Van Hoey, G., Degraer, S., Vincx, M., 2004. Macrobenthic community structure of soft-bottom sediments at the Belgian Continental Shelf. Estuar. Coast. Shelf Sci. 59 (4), 599–613. https://doi.org/10.1016/j.ecss.2003.11.005.

Van Hoey, G., Seghers, S., Festjens, F., Dewitte, B., Vanavermaete, D., Jacobs, L., Wittoeck, J., Hillewaert, H., Lefranc, C., Vanhalst, K., & Hostens, K. (2022). *Influence of the disposal of dredged material on the marine sea-bottom ecosystem in the Belgian Part of the North Sea*.

Verfaillie, E., van Lancker, V., van Meirvenne, M., 2006. Multivariate geostatistics for the predictive modelling of the surficial sand distribution in shelf seas. Cont. Shelf Res. 26 (19), 2454–2468. https://doi.org/10.1016/j.csr.2006.07.028.

Verhalle, J. (2020). HET MARIEN RUIMTELIJK PLAN 2020-2026. In *De Grote Rede* (51st ed., pp. 4–11). www.marienruimtelijkplan.be.

Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89 (8), 2290–2301.

Villéger, S., Miranda, J.R., Hernández, D.F., Mouillot, D., 2010. Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. Ecol. Appl. 20 (6), 1512–1522.

Wilson, W.H., 1991. Competition and predation in marine soft-sediment communities. Annu. Rev. Ecol. Syst. 21, 221–241. www.annualreviews.org/aronline.

Wyns, L., Roche, M., Barette, F., Van Lancker, V., Degrendele, K., Hostens, K., De Backer, A., 2021. Near-field changes in the seabed and associated macrobenthic communities due to marine aggregate extraction on tidal sandbanks: a spatially explicit bio-physical approach considering geological context and extraction regimes. Cont. Shelf Res. 229, 104546.