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Benthic synecology in a soft sediment shelf: habitat contrasts and assembly rules of life strategies

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ABSTRACT: Biological traits of benthic macroinvertebrates from a large area of the North Sea soft sediments were used to explore habitat occupancy within seascapes of contrasting hydrodynamics. The area, the Dutch sector of the North Sea, is mainly composed of 2 habitats: shallow dynamic bottoms of heterogeneous geomorphologies and deep homogeneous muddy bottoms. Higher within-habitat heterogeneity was hypothesized to more specifically select benthic life strategies according to environmental filtering, i.e. through the action of abiotic forces. Functional community patterns were explored through the RLQ method, which relates habitat and trait variables, at different spatial scales of specific seascape heterogeneity, and functional diversity indices were used to shed light on community assembly mechanisms. Locally, 3 associations between habitat characteristics and biological traits were shown to correspond with predictions of life history theories, whereas only 2 emerged when considering all types of seascapes. This spatial scale-dependence was explained by abiotic alternations masked over the larger scale at which all the existing strategies could not be properly disentangled. The relative composition in strategies obeyed specific assembly rules as identified by functional diversity indices. Seascape geomorphology was locally discriminant of functional patterns, and could account for biodiversification, much beyond basic taxonomic counts. Whereas habitats of higher physical stability hosted the taxonomically richest communities, stress or disturbance frequency increased functional variations within communities due to different strategist habitat occupancies. This study proposes a generic mechanism of benthic community structuring in soft sediment shelves.

KEY WORDS: Benthic macroinvertebrate · Biological trait · Life strategy · Assembly rule · Spatial contingency · Stress · Disturbance · Geomorphology

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1. INTRODUCTION

The use of biological traits has become essential to provide sound mechanistic understanding of patterns in species community ecology (McGill et al. 2006). During the last 15 yr, the use of traits in marine ecology has received growing attention, with a productive series of works on various aspects re-

viewed by Beauchard et al. (2017). At present, benthic macroinvertebrates are by far the most studied ecosystem component with traits, since the benthos ensures many ecological functions in the sea floor and provides diverse fundamental and applied research opportunities. For several decades, the use of traits expressing the relations between organisms and sediments ('effect traits'; Lavorel & Garnier 2002) has

been central in major achievements of marine benthic ecology (Rhoads 1974, Pearson & Rosenberg 1978, Solan et al. 2004, Norling et al. 2007, Hewitt et al. 2008, Belley & Snelgrove 2016). More recently, broader perspectives have fostered the use of a wider panel of traits, including growth and reproduction, for studying the relationships between habitat characteristics and community composition (Bremner et al. 2006, Oug et al. 2012, Fleddum et al. 2013, Darr et al. 2014), functional diversity (Bremner et al. 2003, Törnroos & Bonsdorff 2012, Villnäs et al. 2018) and also human-mediated sea floor damages and indicator development (Tillin et al. 2006, Bolam & Eggleton 2014, Bolam et al. 2017, Kenny et al. 2018, Beauchard et al. 2021).

Curiously, the specific use of traits in an evolutionary perspective on identifying life strategies has been much more limited, unlike in terrestrial ecology and limnology (Beauchard et al. 2017). In an organism, a life strategy is a suite of trait modalities that have evolved through the natural selection of abiotic forces and biotic interactions (Stearns 1992). Such traits are necessarily 'response traits' that express the fitness components (growth, survival and reproduction; Lavorel & Garnier 2002), and their modalities are organised in trade-offs due to constraints in energetic allocations in one or the other fitness component (Braendle et al. 2011). The concept of life strategy gained momentum with the advent of gradient theories from the 1970s with the aim at building periodic tables of living forms based on adaptations to environmental variability (Grime 1977, Southwood 1977). Growing interests in assembly rules that determine trait similarity within a community of coexisting species then deepened developments (Keddy 1992, Weiher & Keddy 1995). Through environmental filtering, abiotic forces remove species lacking specified combinations of trait modalities, inducing trait convergences into life strategies, whereas lesser abiotic control leads to trait divergence resulting from increased biotic interactions ('limiting similarity', MacArthur & Levins 1967). Since then, in a wide array of ecosystems, universal life strategies have been recognised to be specific of habitat spatio-temporal characteristics (Grime & Pierce 2012). For instance, *r*- and *K*-strategies are considered the respective adaptive endpoints of a gradient of decreasing disturbance frequency or magnitude in both terrestrial (Pianka 1970) and marine ecosystems (Pearson & Rosenberg 1978); individual growth and population turnover are the main characteristics of these strategies, i.e. fast and slow, respectively.

Another strategy is expected where adversity generates stress, considered for plants by Grime (1977) ('stress resistance') and more generally discussed by Greenslade (1983). Disturbance is here considered to be any discrete event that temporarily disrupts the structure of a habitat (Sousa 1984), whereas stress or adversity is defined as continuous environmental harshness pushing physiological limits forward (Greenslade 1983). The most recent and synthetic considerations on life strategies were largely derived from the advance of fisheries sciences and distinguish 4 strategies through the 'precocial-opportunist-survivor-episodic' (POSE) concept as combinations of juvenile and adult mortalities (Kindsvater et al. 2016). Whereas the opportunistic and precocial categories (high adult mortality in both; low and high juvenile survival, respectively) are respectively equivalent to *r*- and *A*-strategies, episodic and survivor are 2 distinct strategies within the *K*-strategy (both long-lived, with high and low juvenile mortality, respectively).

Although the importance of environmental filtering has been recently reconsidered (Cadotte & Tucker 2017, Thakur & Wright 2017), dominant abiotic structuring of marine benthic communities is expected (Snelgrove & Butman 1994). Water movements in the marine environment sustain strong physical forces through horizontal tidal currents and vertical wave energy transmission that directly affect the sea floor (Hall 1994). In soft sediments, this hydrodynamism, at the basis of ecological succession following physical disturbance, has channelled a long series of works investigating species functional types over spatial changes, holding applicable to chemical disturbance through time (Pearson & Rosenberg 1978, Rhoads & Germano 1982, Nilsson & Rosenberg 2000). Disturbance magnitude, recruitment and community recovery have been the main focusses in this research line (McCall 1977, Santos & Simon 1980, Levin 1984, Barry 1989, Günther 1992, Norkko et al. 2006, Sepúlveda & Valdivia 2017, Gladstone-Gallagher et al. 2021). However, most studies were based on limited spatial extents and restrained to few biological features typical of *r*- and *K*-strategies (i.e. opportunistic/pioneer vs. climax). In recent works involving a larger panel of traits (see first paragraph), the exploration of assembly rules has been largely absent; more specific perspectives on benthic life strategies were applied (Kostylev & Hannah 2007, Darling et al. 2012), but empirical relationships between traits and field data are still lacking to support the evidence of trait convergences into life strategies. Comprehensive investigations on assembly rules should take place at relatively large spatial scales at

which higher habitat heterogeneity better enables the detection of environmental filtering (Weiher & Keddy 1995, Winemiller et al. 2015, Cadotte & Tucker 2017) and should involve large sets of response traits of offspring and adult stages to better account for the wider panel of life strategies (Winemiller et al. 2015).

However, the detection of different life strategies in a given area can be spatial scale-specific according to the phenomenon of 'spatial contingency' (Peres-Neto et al. 2012). Habitat heterogeneity is contingent upon the spatial extent under investigation so that environmental filtering may not be optimal at any spatial scale. In this respect, spatial scale-dependent patterns in benthic functional assemblages should be particularly expected on soft sediment shelves where strong abiotic dynamics shape prominent geomorphological structures of variable spatial extent that create various abiotic contrasts (e.g. tidal velocity, sediment type) at different scales (Huntley et al. 1993, Borsje et al. 2009). In marine benthic ecology, the role of geomorphology has received increasing attention (Baptist et al. 2006, Erdey-Heydorn 2008, Damveld et al. 2018, Holzhauer et al. 2020), but its role in determining associations between abiotic characteristics and organism living modes remains unknown.

In this paper, we explore the relationships between habitat characteristics and biological traits of benthic communities from a large area of the North Sea soft sediments. As a first hypothesis, we assumed that combinations of habitat characteristics should directly select specific combinations of biological traits as life strategies resulting from assembly rules. Then, given the variable geomorphological contrasts encountered on soft sediment shelves, we hypothesized that life strategies should be better discriminated under the highest habitat heterogeneity found in the investigated area. In this way, we explored the implications of geomorphology in the process of environmental filtering as a generic mechanism of benthic community structuring in soft sediment shelves.

2. MATERIALS AND METHODS

2.1. Study area

The study area, the Dutch sector of the North Sea, covers 57 000 km² (Exclusive Economic Zone, EEZ; Fig. 1a). It spreads over the east half of the Southern Bight in the south and extends to the Dogger Bank in the north. Above 30 m deep, south of 54° N, currents from the eastern UK coast and the English Channel

generate high bottom current speeds (>0.2 m s⁻¹) which maintain a coarse sediment mainly composed of mobile sand and prominent geomorphological structures (Fig. 1b). The northern part, 'Oyster Ground', is a deeper (>40 m) area characterised by lower current speeds and a much muddier sediment (Duineveld et al. 1992). Gravel beds are very sparse, and mud content in sand is the main aspect that characterises sedimentary variations. In this cold temperate system, the average bottom water temperature ranges between 9 and 12°C.

2.2. Macrozoobenthic monitoring

We used the data from a yearly monitoring programme of the macrobenthic fauna at 103 sampling stations within the Dutch EEZ that has been coordinated by the Ministry of Infrastructure and Water Management (Rijkswaterstaat 2019) since 1995. Monitoring was continuous until 2010, after which it was conducted less frequently, with the last available data dating from 2012 and 2015 (18 yearly samplings in total). Organisms were sampled between March and June by means of a Reineck boxcorer (1 replicate; 0.068–0.078 m², 15 cm deep), sieved through 1 mm, sorted and identified to the lowest possible taxonomic level. After sieving, organisms were counted and weighed (ash-free dry weight) so that 3 densities per m² were available for analyses: individual organisms, biomass and taxa; see Daan & Mulder (2009) for more details. Data analyses were based on densities of the overall period and averaged per station.

2.3. Environmental descriptors

At each station, particulate organic matter and particulate organic carbon were obtained from a core of the first 3 cm. Habitat descriptors were completed by data from different sources: stratification (van Leeuwen et al. 2015), water depth (EMODnet Bathymetry Consortium 2018) and sediment types (Rijkswaterstaat 2013); primary productivity was obtained from the predictions of the General Estuarine Transport Model – European Regional Seas Ecosystem Model (Baretta et al. 1995); detailed information is provided in Table S1 in the Supplement at www.int-res.com/articles/suppl/m682p031_supp.pdf. Additionally, median bottom current speed and bottom wave energy, calculated over a large part of the monitoring period (monthly basis), were provided by the Deltares Institute (Delft, The Netherlands, P. M. J. Herman

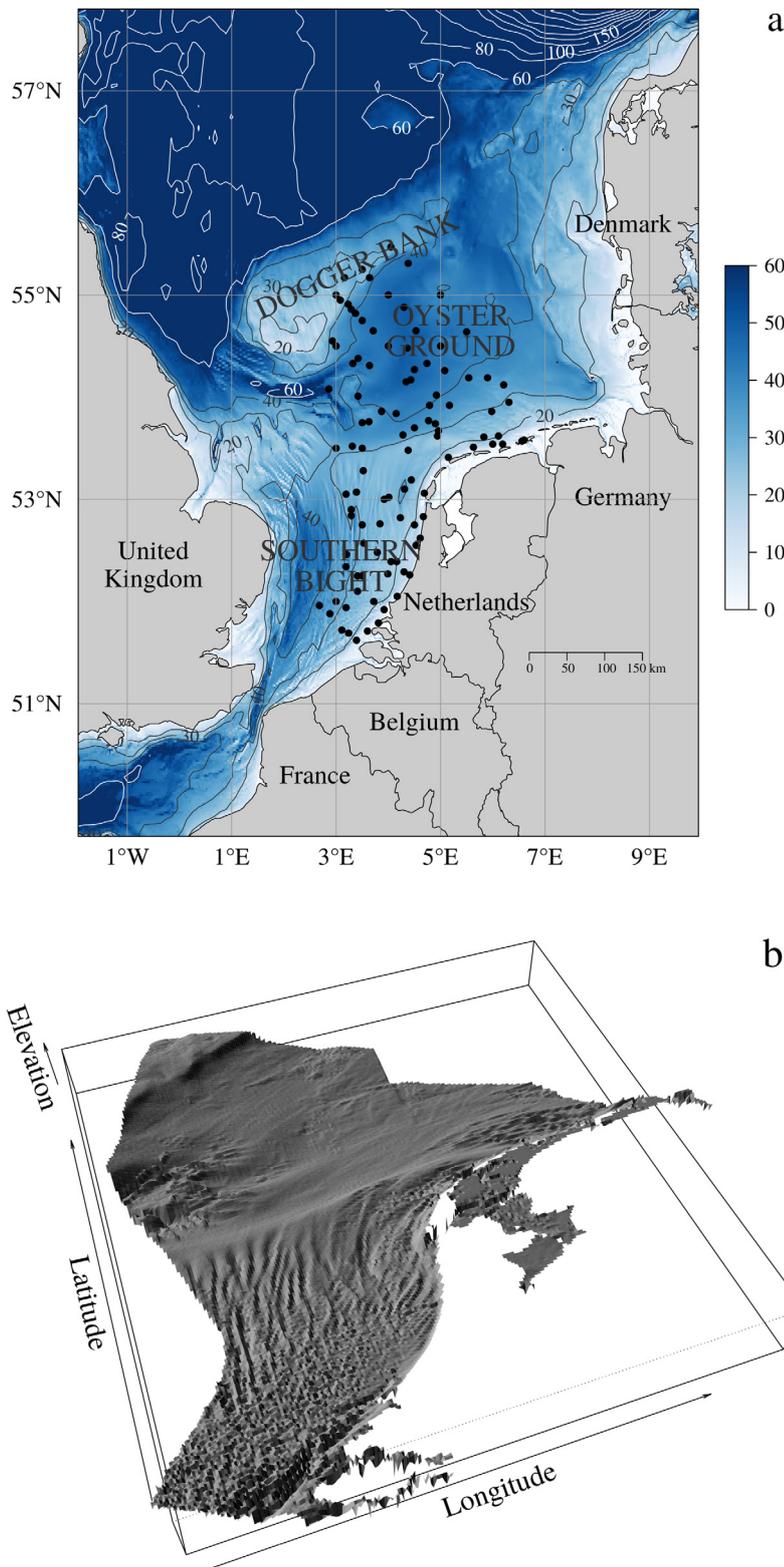


Fig. 1. (a) Study area in the North Sea. Contour lines: isobaths (m); colour bar: depth (m); black dots: sampling stations spread over the Dutch EEZ. (b) Three-dimensional bathymetric close-up of the sampled area within the Dutch EEZ displaying the geomorphological contrasts of the seascapes

a pers. obs.; Cronin 2012). These environmental variables are habitat descriptors traditionally used in marine benthic ecology and can provide a mechanistic understanding of habitat occupancy since they act directly on organism fitness. They were used to test our first hypothesis according to which environmental forces could determine specific combinations of biological traits.

Sea bed geomorphological descriptors were computed and used to underpin both hypotheses. From a bathymetric raster (resolution of 31 684 m²), we considered 3 descriptors of bed-forms: rugosity, representing sea floor roughness; slope as the deviation from the horizontal benchmark; and curvature as the derivative of slope. We then computed a series of bathymetric position indices (BPIs; Lundblad et al. 2006) that account for surrounding geomorphology at a defined spatial scale. A BPI expresses the elevational difference between the location of interest and the surrounding area; it was considered for radii of 800, 500, 400, 200, 100, 50, 25, 10, 5, 3 and 2 pixels, accounting for respectively 142.142, 88.829, 71.071, 35.536, 17.768, 8.884, 4.442, 1.777, 0.888, 0.533 and 0.355 km. A negative BPI indicates that a sampling station is located in a concavity such as trough, whereas a positive value indicates convexity, such as a bank.

b

2.4. Biological traits

Fifteen traits were considered to explore living modes of benthic organisms (Tables S2 & S3). These traits cover the major functions that express fitness components (growth, survival and reproduction) in response to environmental influences (biotic and abiotic). Data were compiled from 502 sources, mostly published peer-reviewed articles (455) and books (17) with additional grey literature (17 academic theses, 10 reports) and a few records from online data bases (3). We gave priority to works on natural history that could

document traits that we considered relevant in terms of fitness expression. Traits comprised ordinal and nominal descriptors that were all qualitatively coded with the modality summarizing the main biological mode within each trait (complete disjunctive coding).

The proportion of documented taxa is a recurrent issue in trait analyses. In this study, the whole fauna was composed of 391 taxa, whereas only 190 were completely documented for traits. We assessed the relevance of the documented faunal data subset by correlation analyses. We compared number of taxa, total individual and biomass densities, calculated per sampling station, separately for the whole data set and for the documented data subset. The 3 indices were significantly and strongly correlated ($r > 0.96$, $p < 0.001$; Fig. S1). Although the number of taxa was substantially lower in the subset documented for traits, individual and biomass densities represented 92 and 96% of the whole data set, respectively. From there, we assumed that the documented subset was structurally representative of the whole data set.

2.5. Data analysis

2.5.1. Habitat identification

Large-scale abiotic contrasts are known to occur in the study area (Duineveld et al. 1992; Fig. 1b), so that in a first analysis, we combined habitat descriptors and fauna to highlight the main community gradients and to derive habitats of different abiotic heterogeneity for further specific biological trait analyses. Firstly, after \ln -transformation, faunal data were processed by correspondence analysis, and habitat descriptors, comprising a mix of quantitative and qualitative variables, were subject to Hill and Smith analysis (Hill & Smith 1976), after which both were combined into a co-inertia analysis (Dray et al. 2003). Whereas depth and wave energy conserved a strong degree of correlation independently of spatial scale, their linear relationships with current speed were strongly scale-dependent. Hence, these 3 descriptors were transformed into categorical variables (each as a series of binary variables) in order to circumvent consequent non-linear constraints. This procedure, although not commonly encountered in the ecological literature, has been known for a long time as a solution to such constraints in multivariate data analysis since relationships between binary variables are necessarily linear (Escoufier & Pagès 1990, Michailidis & de Leeuw 1998, Nishisato 2006). Co-inertia axes encompass the covariant information between habitat descriptors

and fauna so that they express habitat preferences quantified by the RV-coefficient, a multivariate equivalent of the Pearson's r -coefficient (Robert & Escoufier 1976). Habitats were derived from a hierarchical clustering based on Ward's aggregation criterion (Murtagh & Legendre 2014) applied on a Euclidean distance matrix built from the co-inertia axis scores of the sampling stations.

2.5.2. Relationships between habitat descriptors, biological traits and functional diversity indices

In order to test our first hypothesis, we analysed the relationships between habitat descriptors and biological traits that should take place under environmental filtering, over the whole study area and within habitats. We applied RLQ analysis (Dray & Legendre 2008), which builds axes maximizing squared covariances between habitat descriptors (table R, defined on stations) and biological traits (table Q, defined on species) through the faunal link (table L, stations \times taxa) processed by correspondence analysis; prior to RLQ, table R was processed by Hill and Smith analysis and table Q by multiple correspondence analysis (Tenenhaus & Young 1985). The degree of association between table R and table Q is quantified by RLQ inertia, which is the fourth-corner statistic from Dray & Legendre (2008) whose significance under the null hypothesis is tested by row permutations of table L to break the link with table R (model 2) and column permutations to break the link with table Q (model 4). Significances of specific associations between habitat and traits were tested by the procedure from Dray et al. (2014) which combines variables (of tables R and Q) and RLQ axes through the fourth-corner method. Given the multiplicity of tests, a p -value adjustment was done following the false discovery rate method, accompanied by a necessarily very large number of random permutations (99 999). Relationships were considered significant when p -values of both model tests were verified to be < 0.05 (ter Braak et al. 2012).

The RLQ method enables the simultaneous projection of habitat descriptors and traits on the same axes, but also sampling stations and species. Hence, species RLQ axis scores can be considered as synthetic biological traits, expressing only the significantly functional part of the biological data. These scores were used to compute functional diversity indices to verify assembly rules of species coexistence in the synthetic trait space within communities, since pioneer works (see Introduction) predicted trait

convergence (i.e. species close to each other) under environmental filtering (or ‘underdispersion’; Weiher & Keddy 1995). We considered the most independent indices: functional richness, evenness, divergence and dispersion (Villéger et al. 2008, Laliberté & Legendre 2010). These indices, computed per station, were simply used in a correlative way with RLQ axes. RLQ is unbiased compared to other approaches such as the community weighted mean and the species niche centroid that are based on weighted averages and ignore trait variations within communities, which can lead to spurious correlations between environment and traits (Peres-Neto et al. 2017). In this respect, the use of RLQ axes for computing functional biodiversity indices was methodologically unbiased, since these indices express within-community functional structure (Villéger et al. 2008).

2.5.3. Spatial variations and geomorphological implications

Lastly, to support our second hypothesis, we compared the levels of habitat heterogeneity that could maximize environmental filtering within the RLQ patterns. We quantified the extents of spatial variations of the associations between habitat descriptors and traits (hereafter called ‘ecological variations’) that accounted for habitat heterogeneity. We used the approach of Dray et al. (2012) based on Moran’s eigenvector maps (MEMs). MEMs are variables representing independent spatial variations over a surface area and ranked in descending order of spatial wavelength. They are eigenvectors obtained from the diagonalization of a spatial weighting matrix containing linkages between spatial units (i.e. sampling stations). Different functional features of the marine benthos could suggest the use of different linkage methods. For instance, applying the nearest neighbour could justify the relatively important sedentary living mode of benthic macroinvertebrates, whereas other methods involving more links could justify larval dispersal over large extents. As a compromise, we used the Delaunay triangulation. Significant RLQ axis station scores were then modelled through redundancy analysis (RDA) based on the forward selection of MEMs according to Blanchet et al. (2008). Finally, we compared the relative contributions of large- and small-scale MEMs to total explained RLQ variation (adjusted R^2) for each analysed spatial extent.

Within each RLQ pattern, geomorphological descriptors, unlike habitat descriptors, were assumed to be indirect drivers of species distributions so that they

were passively used through correlations with the RLQ axes in order to verify if scale- and shape-specific bed forms could explain ecological variations. Most of the geomorphological descriptors took negative and positive values, and several exhibited right-skewed distributions. Prior to analyses, they were ln-transformed after having been rescaled between 0 and 1.

All analyses were performed in R 4.0.3 (R Core Team 2020): multivariate ordinations and permutation tests with the package ‘ade4’ (Chessel et al. 2004, Dray et al. 2007), functional diversity indices with ‘FD’ (Laliberté et al. 2014) and MEM computations and forward selections with ‘adespatial’ (Dray et al. 2018).

3. RESULTS

3.1. Ecological gradient and habitat description

Co-inertia analysis (Fig. 2) highlighted a main axis encompassing 99% of the variance of habitat descriptors and 99% of the variance of taxa distributions; the 2 multivariate structures being strongly correlated (best correlation obtained with organism individual density; RV-coefficient = 0.70, $p < 0.0001$). Table 1 displays correlations of habitat descriptors on the axis, which reflected a physico-chemical gradient from low dynamics in the central-northern parts (Oyster Ground area; deep, with low current speed and wave energy, and muddy and organic sediment) to high dynamics in the Southern Bight (shallow, with high current speed and wave energy, and coarse sediment). To a lesser extent, the water column was permanently mixed in the south and seasonally stratified in the north. This latitudinal gradient was not entirely monotonous as, in the northernmost part, the Dogger Bank exhibited high axis scores (Fig. 2). Although experiencing low current speed, the shallow sea floor of the Dogger Bank was substantially exposed to wave energy that maintained a sandy sediment of lower organic content. The clustering of station axis scores (Fig. 2) clearly expressed this habitat dichotomy, distinguishing the deep central-northern part (low dynamics) from the southern shallow part including the rise of the Dogger Bank (high dynamics).

3.2. Biological trait analysis of the whole area

Over the whole area, the RLQ pattern was significant only when using organism presence–absence (Table 2).

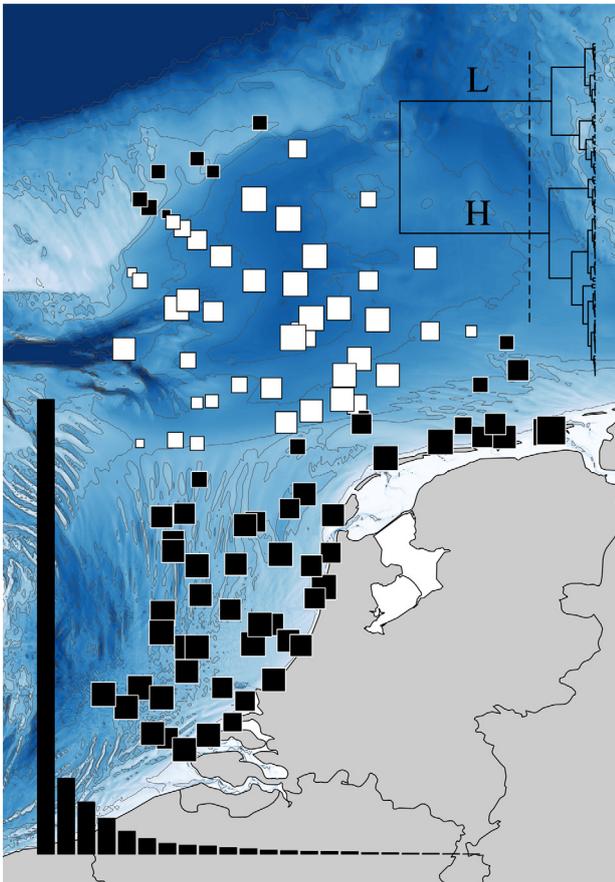


Fig. 2. Co-inertia analysis combining habitat descriptors and taxon distributions. The bar diagram illustrates eigenvalues, showing a major first axis (64%). Squares represent the first axis score of the sampling stations. White squares: low scores; black squares: high scores; square sizes are proportional to the deviation from the mean axis score [0, 0]. The dendrogram shows sampling station axis score clustering; 'L' and 'H': low and high dynamics, respectively. The L-cluster includes only negative axis scores (white squares), while the H-cluster includes only positive axis scores

The pattern was limited to a single axis (84% of total inertia), on which the only significant correspondences between habitat descriptors and biological traits were found (Table 3). The analysis reproduced the first axis of the previous co-inertia analysis without much distortion (explaining 96% of table R variance), with a similar expression of habitat descriptors (Table 3). All organism and taxonomic densities decreased from low to high dynamics (Table 3). Richer communities had larger functional volumes (functional richness) and lowest functional evenness. Functional dispersion was strongly characteristic of high dynamics, positively correlated with the first axis.

Out of 15 traits, 10 significantly co-structured the RLQ axis (explaining 75% of table Q variance). How-

Table 1. Co-inertia analysis combining habitat descriptors and taxon distributions; Pearson's r -correlations between habitat descriptors and the first co-inertia axis. Descriptors are arranged in increasing order of correlation value. TR: transitional; SS: seasonally stratified; IS: intermittently stratified; PM: permanently mixed; FI: freshwater influence. See Table S1 for detailed information on descriptors

Descriptor	r	p
Particulate organic carbon	-0.80	<0.001
Depth — very deep	-0.72	<0.001
Particulate organic matter	-0.67	<0.001
Sediment — muddy	-0.64	<0.001
Wave — very low	-0.61	<0.001
Current speed — very low	-0.60	<0.001
Wave — low	-0.54	<0.001
Stratification — TR	-0.50	<0.001
Stratification — SS	-0.24	0.014
Current speed — low	-0.19	0.060
Depth — deep	-0.17	0.086
Sediment — mixed	-0.14	0.158
Stratification — IS	0.17	0.078
Current speed — intermediate	0.22	0.024
Depth — very shallow	0.24	0.014
Stratification — PM	0.28	0.004
Stratification — FI	0.29	0.003
Wave — intermediate	0.31	0.001
Sediment — coarse	0.32	0.001
Sediment — sandy	0.32	0.001
Depth — shallow	0.35	<0.001
Wave — high	0.36	<0.001
Current speed — high	0.38	<0.001
Current speed — very high	0.42	<0.001
Wave — very high	0.44	<0.001
Depth — intermediate	0.47	<0.001
Primary productivity	0.50	<0.001

ever, when looking at trait modality positions (Fig. 3), most of the pattern was structured by a specific set of modalities covarying together to the right side of the axis (high station scores in Fig. 2, high dynamics), in opposition to most other modalities. These were very small body mass (Fig. 3a), swimming ability (Fig. 3b), surficial living mode (Fig. 3c), earliest maturity (Fig. 3f), continuous reproduction (Fig. 3g), and release of a few large juvenile offspring after internal incubation (i.e. viviparity; Fig. 3h–m). Correlations of individual modalities with RLQ axes and their significances are provided in Table S4. These biological attributes were strongly specific to amphipods (e.g. *Ampelisca* spp., *Bathyporeia* spp., *Urothoe* spp.), isopods (e.g. *Eurydice pulchra*, *Idotea linearis*) and mysids (e.g. *Gastrosacus spinifer*, *Mesopodopsis slabberi*, *Schystomysis* sp.). Some trends in other traits appeared but remained more suggestive than significant (e.g. life span, decreasing toward high dynamics).

Table 2. Summary of RLQ analyses. Number of axes: only axes on which habitat descriptors and traits are significantly related are retained for interpretation; projected inertia: variance of habitat descriptors (table R) and biological traits (table Q) expressed on RLQ axes; Chessel's correlation: fourth-corner correlation as a proportion of its optimum. Whole area and low dynamics analyses are significant only with presence–absence, high dynamics with individual organism density. See Section 2.5.2 for a description of the models

		Whole area	Low dynamics	High dynamics
Significance (p)	Model 2	0.00001	0.00001	0.00001
	Model 4	0.03399	0.02034	0.03692
Number of axes		1	1	2
Projected inertia (%)	Table R	96	65	88
	Table Q	75	47	70
Chessel's correlation R-Q	Axis 1	0.25	0.31	0.32
	Axis 2			0.32

Moreover, and apart from these specific attributes, between-habitat trait ordination was almost not affected by the abiotic differences (Fig. 3; no discrimination between grey and black distributions). This was likely explained by the lack of species specificity among the 2 habitats: 152 and 167 taxa were found in low and high dynamics, respectively, with 129 in common (only 38 not shared), illustrated by large range overlaps of the 2 faunas. By contrast, within-habitat coefficients of variation of taxon richness largely differed, with only 8% in low dynamics and 31% in high dynamics. Also, averaged individual organism frequencies per trait modality revealed noticeable differences between the 2 habitats (Fig. S2). Additional to differences in mean densities, a major feature was the systematically larger within-modality variation in high dynamics (SD = 5.26 against 2.52 in low dynamics), indicating higher functional heterogeneity among communities in high dynamics, and advocating for within-habitat analyses.

3.3. Biological trait analysis in low dynamics

RLQ analysis on low dynamics data revealed only one axis significantly related to both habitat descriptors and traits (Table 2); again, only organism presence–absence yielded a significant pattern. Only 9 traits were significantly expressed and included mostly modalities identifying the peculiar biology of the small crustaceans previously highlighted in the whole-area analysis (Table 3). Due to their redundancy, the results are not further detailed, and graphical displays are provided in the Supplement (Figs. S3 & S4). However, it should be noted that a prominent second axis

was found to be related to several habitat descriptors (Fig. S3), and, although not significant, a few trait modalities were differentiated in the upper part of this axis, characterising sessile living mode and release of large number of small eggs in the lowest dynamic conditions of the area (Fig. S4).

3.4. Biological trait analysis in high dynamics

The RLQ pattern of high dynamics was significant only when using individual densities and showed that 2 clear gradients could be considered

(Table 2, Fig. 4a). The first axis identified a large extent of southern offshore stations of intermediate depth and characterised by high current speed and lower organic content (Fig. 4b). Independently, the second axis opposed shallower stations undergoing very high wave energy with higher primary productivity (lower part of the axis) to deeper muddy stations of minimum current speed and lower wave energy (upper part). This second axis was much less spatialized; lower hydrodynamics (i.e. current and wave), although characteristic of the Dogger Bank in the north, were also found patchily distributed within the most hydrodynamic extent of the overall study area (Fig. 4c). In summary, 3 sub-habitats were encountered here: stations stressed by high current speed (Fig. 4a, right and bottom-right), stations undergoing strong wave action (Fig. 4a, bottom to bottom-left) and stations of lower hydrodynamics (Fig. 4a, to the top); Fig. S5 provides detailed distributions of all habitat descriptors.

These sub-habitats were strongly characterised by benthic functionalities as all biological traits significantly corresponded to the axis scores (Table 3). The very small short-lived crustaceans identified in the whole-area analysis were typical of high current speed on the right side of the first axis (Fig. 5). In opposition, the other taxa were spread mainly along the second axis, from disturbed to more physically stable conditions. Between these latter two, disturbed conditions were characterised mainly by smaller and shorter-lived taxa (Fig. 5b,f). Tubicolous living mode was most characteristic, represented by *Capitella capitata*, *Heteromastus filiformis*, *Mediomastus fragilis*, *Polydora* sp., *Prionospio* sp., *Spio* spp. and *Pygospio elegans*. This living mode was associated with spermcasting (Fig. 5j), typical in many

Table 3. RLQ analyses, significance of variables on the axes. Traits and habitat variables were tested according to the fourth-corner method combined with RLQ from Dray et al. (2014). Reported statistics ('Stat.') are pseudo- F for qualitative variables (depth, current speed, wave energy, stratification, sediment and each trait) and Pearson's r for quantitative variables (all other variables); see Tables S1 & S2 for detailed information on habitat and trait variables, respectively. Relationships of geomorphological descriptors with RLQ axes were assessed by Pearson's r ; within parentheses, radius based on which bathymetric position indices (BPIs) were calculated. Missing values, encountered for small BPIs, indicate that there was no variation in the descriptor (0 as unique value), preventing computation; for functional divergence, there is no possible calculation for unidimensional space

Data	Variable	– Whole area –		– Low dynamics –		– High dynamics –			
		Axis 1		Axis 1		Axis 1		Axis 2	
		Stat.	p	Stat.	p	Stat.	p	Stat.	p
Habitat	Depth	18.658	0.00413	2.479	0.04660	21.012	0.01347	17.046	0.02092
	Current speed	19.494	0.00413	1.360	0.26278	27.171	0.00368	14.381	0.03511
	Wave energy	20.136	0.00413	3.547	0.01883	16.989	0.02092	11.477	0.04796
	Stratification	11.035	0.00462	3.543	0.00553	5.826	0.09244	6.077	0.04796
	Sediment	15.483	0.00413	10.525	0.00016	2.326	0.47857	8.480	0.01555
	Particulate organic matter	-0.082	0.00987	-0.044	0.03325	0.005	0.85834	0.040	0.11620
	Particulate organic carbon	-0.106	0.00817	-0.093	0.00027	-0.094	0.01074	0.006	0.85834
	Primary productivity	0.080	0.00802	-0.010	0.62008	0.055	0.04018	-0.081	0.00346
Traits	Body mass	9.815	0.04467	0.895	0.53690	15.891	0.00057	10.600	0.00943
	Motility	26.099	0.00045	4.994	0.00510	32.779	0.00006	6.769	0.09295
	Burrowing depth	24.461	0.00052	3.963	0.00851	20.794	0.00027	4.220	0.25289
	Feeding type	5.988	0.23410	0.597	0.70183	13.626	0.00152	3.997	0.26460
	Life span	8.579	0.09791	0.608	0.66929	10.622	0.01968	21.525	0.00017
	Age at maturity	15.143	0.02813	0.083	0.91250	11.644	0.02890	30.715	0.00019
	Reproductive frequency	88.792	0.00030	10.866	0.00232	34.502	0.00152	15.160	0.03305
	Annual fecundity	8.362	0.08762	3.506	0.00840	25.318	0.00006	4.895	0.17303
	Fertilization	21.711	0.00514	5.369	0.00844	20.317	0.00172	3.090	0.35027
	Offspring type	24.888	0.00168	2.990	0.08151	48.120	0.00006	7.727	0.09168
	Offspring size	14.473	0.01279	5.849	0.00150	24.459	0.00010	3.811	0.28190
	Offspring protection	17.071	0.00514	7.074	0.00150	6.979	0.09295	8.923	0.04688
	Offspring development	20.391	0.00050	3.512	0.01060	20.006	0.00006	6.727	0.07967
	Offspring benthic stage duration	10.294	0.09448	7.434	0.00150	22.298	0.00112	21.849	0.00115
	Offspring pelagic stage duration	6.311	0.25477	0.121	0.91250	40.818	0.00006	1.800	0.53427
Community	Individual density	-0.463	<0.00001	0.042	0.79389	-0.392	0.00164	0.229	0.07361
	Biomass density	-0.267	0.00649	-0.520	0.00049	-0.696	<0.00001	-0.148	0.25113
	Taxonomic richness	-0.697	<0.00001	0.113	0.48213	-0.186	0.14782	0.598	<0.00001
	Functional richness	-0.703	<0.00001	-0.484	0.00135	-0.288	0.02297	0.155	0.22975
	Functional evenness	0.673	<0.00001	-0.359	0.02111	-0.424	0.00060	-0.002	0.99016
	Functional divergence					0.227	0.07637	-0.377	0.00256
	Functional dispersion	0.747	<0.00001	0.668	<0.00001	0.424	0.00060	-0.174	0.17602
Geomorphology	BPI 02 (355 m)	0.138	0.16434			0.180	0.16230	-0.140	0.27683
	BPI 03 (533 m)	0.110	0.26714			0.117	0.36379	-0.133	0.30416
	BPI 05 (888 m)	0.099	0.31933			0.220	0.08611	-0.011	0.92952
	BPI 10 (1777 m)	-0.029	0.76955	0.245	0.12214	0.044	0.73366	0.148	0.25157
	BPI 25 (4442 m)	-0.048	0.62795	0.104	0.51720	-0.057	0.65720	0.157	0.22279
	BPI 50 (8884 m)	-0.036	0.71632	-0.021	0.89558	-0.135	0.29571	0.176	0.17042
	BPI 100 (17 768 m)	0.022	0.82265	0.237	0.13521	-0.245	0.05531	0.110	0.39586
	BPI 200 (35 536 m)	0.220	0.02572	0.297	0.05931	-0.338	0.00714	-0.119	0.35594
	BPI 400 (71 071 m)	0.470	<0.00001	0.548	0.00021	-0.411	0.00091	-0.204	0.11213
	BPI 500 (88 750 m)	0.543	<0.00001	0.567	0.00011	-0.496	0.00004	-0.218	0.08826
	BPI 800 (142 142 m)	0.570	<0.00001	0.534	0.00032	-0.543	0.00001	-0.149	0.24849
	Rugosity	0.263	0.00732	-0.266	0.09275	0.289	0.02249	-0.009	0.94312
	Slope	0.489	<0.00001	-0.098	0.54373	0.129	0.31662	-0.374	0.00276
	Curvature	0.072	0.46835	-0.059	0.71270	0.167	0.19461	-0.034	0.79228
	PCA axis 1	0.166	0.09344	-0.513	0.00060	-0.172	0.18069	0.010	0.94087
	PCA axis 2	0.411	0.00002	0.180	0.25918	-0.527	0.00001	-0.083	0.52037

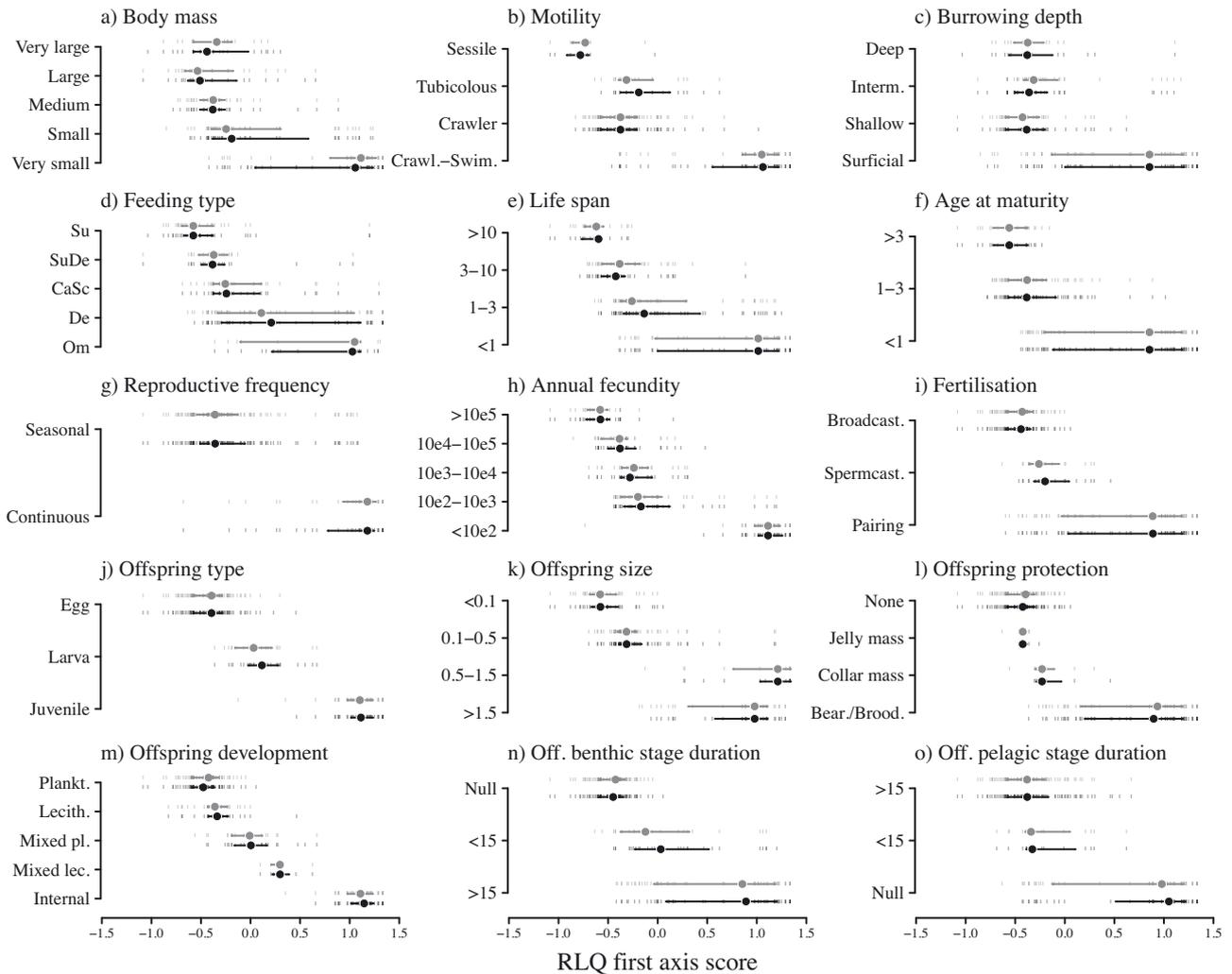


Fig. 3. Whole-area RLQ analysis, trait modality positions along the first axis. Dots, median values of species positions (vertical dashes); bars extend from 25th to 75th percentiles. Grey, low dynamics; black, high dynamics. From left to right of the RLQ axis: increase in current speed and wave energy. Feeding types are Su: suspension feeder; De: deposit feeder; CaSc: carnivore-scavenger; Om: omnivore. Life span and age at maturity in years; annual fecundity, number of offspring from <100 to >100000; offspring size in mm; offspring benthic and pelagic stage duration in days

sedentary worms of mixed offspring development which brood their clutches for a short time until larval release (mixed lecithotrophic; Fig. 5k,m-o). These reproductive attributes were also encountered in co-occurring decapods such as *Carcinus maenas*, *Corystes cassivelaunus*, *Crangon crangon*, *Diogenes pugilator*, *Liocarcinus* sp. and *Pagurus bernhardus*, releasing large planktotrophic larvae after a long brooding incubation (mixed planktotrophic). The upper part of the axis, toward lower dynamism, was characterised by taxa of extended life span with later maturity (Fig. 5b,f,g). These characteristics were associated with reproductive modes lacking parental care, through seasonal broadcasting of numerous small pelagic eggs (Fig. 5h-l). Large bivalves

were typical of this strategy, well represented by *Arctica islandica*, *Ensis* spp., *Mya* spp. and *Spisula* spp., although phylogenetically distant taxa exhibited similar combinations of attributes, like echinoderms (*Echinocardium* sp., *Acrocnida brachiata* and *Amphiura* spp.) and polychaetes (*Glycera* sp. and *Streptosyllis websteri*). There was no clearly identified feeding type here. However, suspension feeding seemed slightly more specific compared to carnivory, more centrally positioned along the second axis (Fig. 5e). Globally, there was a greater burrowing ability among the taxa from the left side of the plane than among those from areas of high current speed, mainly restricted to the sediment surface (Fig. 5d).

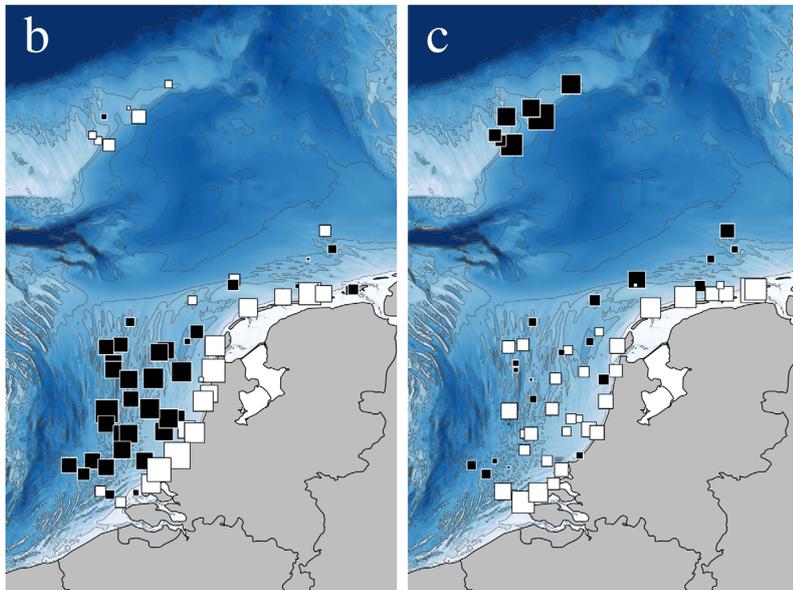
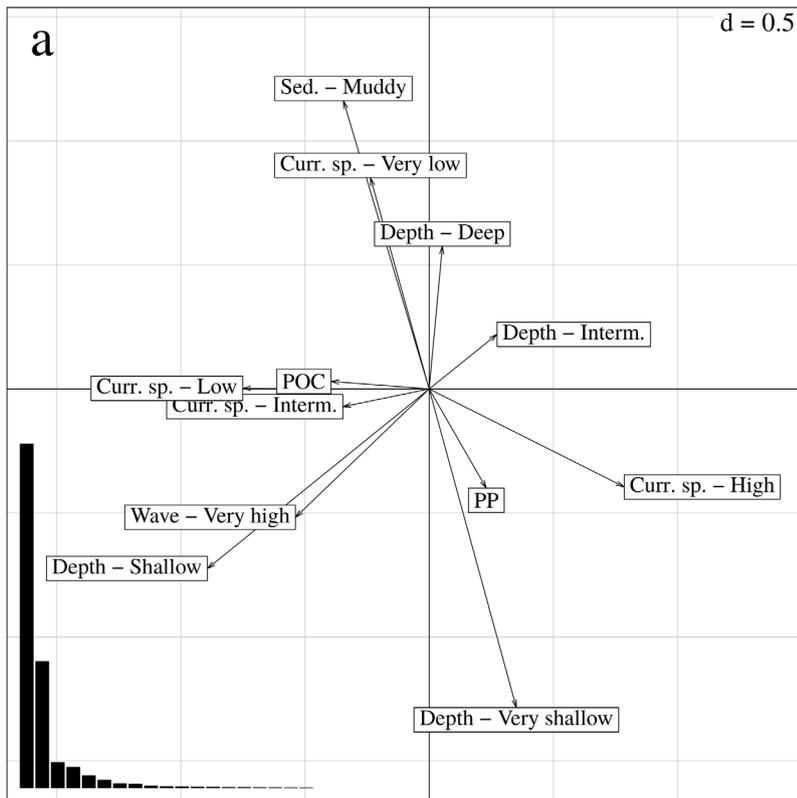


Fig. 4. RLQ analysis of the high-dynamics habitat. (a) Habitat descriptors projected onto axes 1 and 2; 'd' indicates the grid scale; bar diagram, eigenvalues (axis 1, 62%; axis 2, 23%); for clarity, only the significant modalities of qualitative variables are shown (according to Table S4). Curr. sp.: current speed; interm.: intermediate; POC: particulate organic carbon; sed.: sediment; PP: primary productivity. (b) Station axis score 1. (c) Station axis score 2. White squares, low scores; black squares, high scores; square size is proportional to the deviation from the mean

Fig. 5a provides a synthetic representation of the distributions of life strategies; 4 groups were chosen for an optimal description. Typical of high current speed, group 1 represented $25 \pm 15\%$ (SD) of the average total individual density. Group 2, less functionally specific, consisted in the basis of species assemblages, representing $59 \pm 16\%$. Groups 3 and 4 accounted for 7 ± 6 and $9 \pm 13\%$ of densities, respectively. Total individual and biomass densities were limited by high current speed, and taxonomic richness increased with less physical constraints toward group 4, significantly and positively correlated only with the second axis (Table 3). In high current speed, communities were more functionally dispersed and less functionally even. Functional divergence increased from the top (lower hydrodynamics) to the bottom (wave action) of the second axis.

3.5. Spatial structuring of ecological variation

The 3 RLQ patterns were significantly structured according to MEM predictions (Fig. 6a; Table S5). In spite of variable degrees of spatialization (adjusted R^2 ranging from ca. 0.7 to 0.9), a major outcome was the explanatory dominance of MEM 1 in the whole-area RLQ compared to within-habitat RLQs. Whereas MEM 1 explained two-thirds of the variation of the whole-area pattern, it only explained ca. 10 or 30% of within-habitat patterns, for which the additions of several MEMs of higher ranks (smaller scales) were necessary to predict a substantial amount of the total ecological variation. Fig. 6b–d displays the amounts of predictions per class of spatial variation (wavelength) and shows that small- to very small-scale ecological variations dominate the within-habitat patterns compared to the whole-area pattern.



Fig. 5. RLQ analysis of the high-dynamics habitat. (a) Species clustering for synthetic interpretation. (b–p) Distributions of trait modalities (ellipses) respective to each trait (windows); dots, taxon positions; trait modalities are positioned at the gravity centre of their respective taxa. 'd' indicates the grid scale. Feeding types are Su: suspension feeder; De: deposit feeder; CaSc: carnivore–scavenger; Om: omnivore. See Table S2 for detailed information on trait modalities

3.6. Relationships with seascape geomorphology

An outcome common to the 3 RLQ patterns was the large absence of significant correlations with individual small-scale BPIs (Table 3). Only large-scale ones,

with slope and curvature, exhibited significant associations, as expressed by each first PCA axis (Fig. S6). However, second PCA axes from whole-area and high-dynamics habitat provided a synthetic opposition between small- and large-scale BPIs (Fig. S6c &

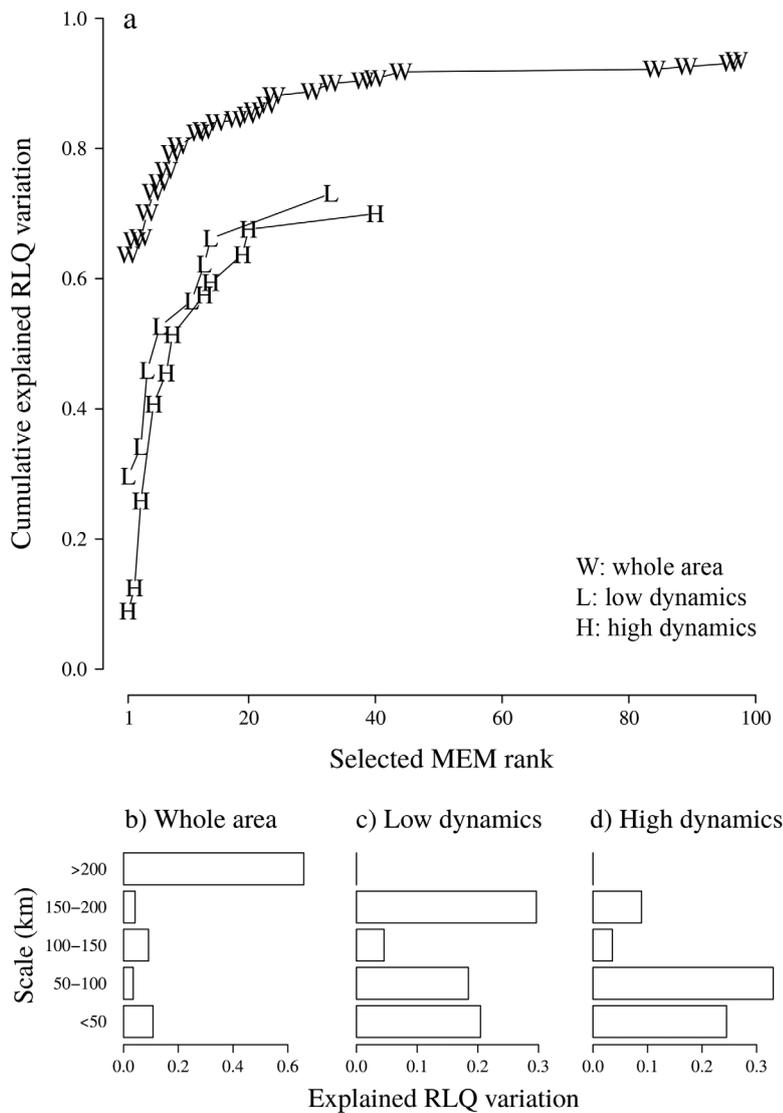


Fig. 6. Spatial structuring of RLQ patterns: (a) x-axis, Moran's eigenvector maps (MEMs) ranked by descending order of magnitude in spatial variation; y-axis, explained RLQ variation by selected MEMs (adjusted R^2), and cumulated across MEMs. Note that a total of 102 MEMs are derived from the whole area that comprises 103 stations (n stations $- 1$); similarly, 40 MEMs are from low-dynamics areas and 61 are from high-dynamics areas; only the significant MEMs are considered here. (b–d) Explained RLQ variation by class of spatial wavelength

Fig. 6c), and indicating significantly higher values of small-scale BPIs in high dynamics (right side of the first RLQ axis of both whole-area and high dynamics). Hence, these small-scale geomorphological variations were concordant with the dominant small ecological variations observed in the high-dynamics habitat (Fig. 6). This supported the role of local shelf geomorphology that indirectly generates abiotic heterogeneity, and consequently optimal environmental filtering of most diversified trait convergences (i.e. Fig. 4).

4. DISCUSSION

4.1. Importance of the type of organism density

The results showed that the type of organism density in table L can be determinant to detect significant relationships between biotic and abiotic components. In no case did biomass density lead to significant habitat–trait relationships. Over the whole area, only presence–absence enabled the detection of significant relationships given the important overlaps of species ranges and the high number of species found in both habitats, and along which taxonomic richness was more responsive than individual and biomass densities (Table 3). Similarly, the better response of presence–absence in the low-dynamics habitat can be explained by the high abiotic homogeneity, firstly, marked by the absence of 7 habitat states (Table S4). Secondly, individual organism densities per trait modality were twice more variable in the high-dynamics habitat (Fig. S2), which exhibited a more diversified abiotic pattern, and for which only individual density led to a significant RLQ pattern. In this habitat, the unique responsiveness of individual density suggests an effect of density dependence, as corroborated by its higher spatial complexity, whereby geomorphological variations may be locally more beneficial to species widely distributed across the seascape. The absence of responsiveness from biomass den-

sity is consistent with the work of Bijleveld et al. (2018), who did not find any strong relationship between species biomass and occupancy in the Wadden Sea, a highly dynamic system at the southeastern edge of our study area; the authors speculated that biomass might be more dependent on species-specific life history constrained by temporal unpredictability such as adult survival and recruitment success (Beukema 1982). Our outcomes suggest that demographic processes (i.e. individual density) may be more determinant than production

(i.e. biomass density) in benthic functional patterns as concluded by Bolam et al. (2002). Nevertheless, as shown in the high-dynamics pattern, total biomass community, negatively correlated to the first RLQ axis, can be indicative of a stress effect on biological production (Table 3).

4.2. Benthic life strategies

In each of the 3 RLQ analyses, the first axis captured the main functional singularity of the patterns, clearly discriminating the small surface-dwelling crustaceans, identified as group 1 in the high-dynamics analysis. The taxa from this group have a very small biomass and they generally do not exceed 1 cm in body length. Their fecundity is minimal, as direct development leads to the release of juveniles larger than 1 mm, which translates a large reproductive allocation during a short life in an environment exposed to predation. This ensures a high juvenile survival rate that compensates for high adult mortality as encountered in amphipods (Sainte-Marie 1991). This fast living mode was systematically associated with high current speed from the sandy bottom. Experimental evidence confirmed strong adaptations of amphipods to high current speeds and catastrophic drift through physical displacement (Grant 1980), supported here by strong swimming ability in group 1 (Table 3, Fig. 5c; Table S4). Affinity of these organisms for mobile sands has been reported in other shallow coastal areas (Dahl 1952, Sameoto 1969, Oliver et al. 1980) as well as on deep continental slopes (Thistle et al. 1985). These observations suggest the concept of *A*-strategy, achieving reproductive success as fast as possible given adverse conditions (Greenslade 1983). Although this group was taxonomically very homogeneous (i.e. mostly amphipods, cumaceans and mysids), it comprised 1 non-crustacean taxon, the brittle star *Amphipholis squamata*, exhibiting similar growth and reproductive features and also found in high dynamics, suggesting a functional convergence despite phylogenetic distance.

A-strategy was detected at the 2 investigated scales, whereas local habitat heterogeneity was necessary to detect other strategies, especially along the second RLQ axis of the high-dynamics pattern. Unlike group 1, isolated by very specific trait modalities, the other groups were arranged along the second axis following a biological continuum, opposing 2 extreme and more familiar functional types according to the *r*-to *K*-selection continuum (Pianka 1970), from group 3 to group 4, respectively. Although the properties of

these strategies can be widely variable and even confusing in the ecological literature, life span and associated age at sexual maturity generally enable to discriminate *K* from *r*. Also, body size is generally considered to be correlated to these traits, but body mass modalities, even if significant on both axes, were not perfectly positioned in an ordinal way along the second axis (Fig. 5b). However, growth rate, a concurrent correlate of the *r*-*K* concept, available for 76 taxa, was significantly and negatively correlated to the second axis (Fig. S7; $r = -0.51$, $p < 0.001$), whereas no link appeared with the first axis ($r = 0.10$, $p = 0.411$). Indeed, relatively short-lived species from group 3 could exhibit remarkable sizes among crabs (e.g. *C. maenas*) and nereid worms (e.g. *Alitta virens*); by contrast, the emblematic North Atlantic quahog *Arctica islandica* from group 4, of comparable body mass, does not reach the age at maturity before 5–10 yr old, more than the life span of the 2 former species. Reproductive traits have also been considered discriminant of the 2 strategies, like high fecundity in *r*-strategists and low fecundity with parental cares in *K*-strategists in general (Southwood 1977, Greenslade 1983) and more specifically in the marine benthos (Giangrande et al. 1994, Ramirez Llodra 2002). Our results are contradictory, since fecundity suggests an increasing trend from group 3 to group 4, at least along the first axis (Fig. 5i), and more costly parental care in *r*-like taxa (Fig. 5m). Here, we argue that these historical and influential considerations were built on generalities either restricted to terrestrial ecology or mainly derived from fish ecology that may have been limited, especially in the absence of empirical evidence in the marine benthos. This requires some clarification based on new advances in the field.

Whereas *A*-strategists (group 1) are equivalent to the precocial type of the POSE concept (Kindsvater et al. 2016), the *K*-like taxa (group 4) are very consistent with the episodic type: large bodied and broadcasting large numbers of small eggs, with consequently a high offspring mortality, whereas larval settlement followed by successful slow growth leads to greater adult survival. This is typical in long-lived bivalves (Beukema et al. 2001, Ridgway & Richardson 2011, Gerasimova & Maximovich 2013), including those positioned in the upper section of our *r*-*K* axis. Given the high offspring vulnerability, successful reproduction is rarely achieved, which requires an extended life span to ensure a minimum number of successes when environmental stochasticity (e.g. temperature, planktotrophy, predation) enables it. Our results indicate that late sexual maturity is a cor-

relate of this strategy, although long-lived (>10 yr) *Chamelea striatula*, *Dosinia* spp. and *Mytilus edulis* can already spawn at 1 to 2 yr old; similarly, *Echinocardium* sp. (mainly represented by *E. cordatum*), matures at 3 yr in the North Sea, but at only 2 yr old further south. On the first axis opposing *A*- to *r*- and *K*-types, and suggestively along the second axis, suspension feeding also converges to an episodic adaptation in intermittently available food resource known to induce episodic reproductive success over the long term (Beukema et al. 2001).

Conversely, taxa from group 3 exhibited characteristics of *r*-strategy of which fast growth is most indicative. Also, tubicolous and other worms encountered in this group (capitelids, nereids, spionids) are known to persist in disturbed environments by optimizing recruitment during their short life. As indicated in our results, a typical reproductive feature of these taxa is the release of benthic jelly egg masses (that can be brooded inside tubes) through mixed development. This provides protection on the sea floor until an advanced larval stage emerges in the plankton once mortality rate is minimized (Pechenik 1990), after which a brief lecithotrophic pelagic stage, lasting from a few hours to a few days, avoids dispersal too far from the right habitat at the right time (Bhaud & Duchêne 1996). Taxa like *C. capitata*, *H. filiformis*, *Kurtiella bidentata*, *Mediomastus fragilis*, *Polydora* sp. and *Spio* spp., which are highly abundant in early ecological succession stages, are known to massively colonize disturbed and defaunated environments (Diaz & Rosenberg 1995). Most of the taxa of group 3 have been reported as either opportunistic or pioneer following disturbance and are consequently *r*-selected species (Grassle & Grassle 1974, Pearson & Rosenberg 1978, Rhoads et al. 1978, Reise 1982). Recruitment in such taxa can be paced by seasonally predictable wave height or ensured against inter-annually unpredictable disturbance through other attributes such as an extended spawning season (Grassle & Grassle 1974, Barry 1989). In their thorough review on marine benthic life strategies, Giangrande et al. (1994) proposed ontogenetic development as a determinant of the *r*-*K* concept. Progenesis and neoteny were hypothesized to be indicative of, respectively, *r*- and *K*-strategies, but our results indicate the opposite in regard to dominant oviparity in *K*, and manifest release of larger offspring in advanced stages of development in *r*, with the most extreme neoteny in the *A*-strategy. Additionally, high fecundity, usually associated with progenesis, has been considered to be characteristic of the *r*-strategy, contradicting Fig. 5i, which sug-

gests the opposite. Our results are consistent based on energetic considerations whereby offspring protective allocation should be achieved at the expense of fecundity as evidenced in marine fishes ('periodic' type; Winemiller & Rose 1992) and spotlighted by Giangrande et al. (1994) as an alternative model for the benthos. Moreover, the presence of the shore crab *C. maenas* in group 3 contrasts the results given its high fecundity (>10⁵ larvae), but its growth rate and remaining reproductive attributes confer it the particular nature of opportunistic species and successful invader (Audet et al. 2008). More generally, *r*-selected species dwell in highly variable environments where population size and recruitment can be poorly correlated (Kindsvater et al. 2016), so that minimum offspring advantage (protection or release at an advanced stage) must be required to ensure the persistence of the population in the long term.

Regarding the POSE concept, the question of the survivor strategy, indiscernible in our results, remains. Even though taxa from group 4 (*K*-like) exhibited key determinants of this strategy (slow growth, late maturity, long life, large body), their excessive fecundities and protogenic ontogeny did not match expectations of survivors for which both adult and offspring mortalities are low (Kindsvater et al. 2016). For instance, *Nephrops norvegicus*, found in low dynamics, is a slow-growing species that also provides substantial parental care (brooding) at the expense of fecundity (10³–10⁴ released larvae). However, this species was found only twice, since the boxcorer is not designed to capture such a large organism. By extension, we could speculate that in benthic marine invertebrates, survivors can be found mostly in the mega-benthos. Associating mega-benthos in future studies may help concluding on body size for which distinctions between *r* and *K* were not clear in our results. At least, in the absence of adapted survey data, our findings suitably related to the endobenthos and body size-limited epibenthos correctly match predictions of the habitat template concept (Greenslade 1983, Southwood 1988), aligned with other models such as Grime's triangle derived from vegetation ecology (Grime 1977).

4.3. Assembly rules

In general, higher organism densities and numbers of taxa were found in deeper areas of lower hydrological dynamism, consistently with the stability-time hypothesis (Sanders 1968), according to which higher physical stability enables more individual

organisms to survive, consequently benefiting higher numbers of species. In the timing of a life span, disturbance frequency can modulate reproductive success by acting on key traits like age at sexual maturity, followed by some delays for ensuring effective recruitment (Lytle 2001). The species-richer low-dynamics habitat is indeed proportionally composed of twice more individual organisms of late maturity (>3 yr) or extended life span (>10 yr; Fig. S2) that characterise the episodic strategy to cope with fluctuations in food resources due to possible stratification in this deep area that can happen episodically (van Leeuwen et al. 2015). Over the whole area, low current speed and wave energy also benefitted more diverse combinations of trait modalities as indicated by higher functional richness, the community functional volume in the trait space (Table 3). This outcome is consistent with the lack of significant separation between *r*- and *K*-strategies in deep, low-dynamics habitat where both coexist.

Although the decrease in functional richness toward *A*-conditions over the whole area could match early expectations of environmental filtering ('trait underdispersion', Weiher & Keddy 1995), the systematic increase in functional dispersion is contradictory, *A*-strategists coexisting with others (e.g. group 2), hence revealing some functional heterogeneity in spite of environmental adversity. In the high-dynamics habitat, divergence (niche specialisation, how far species occur from the mean distance from the community centroid), increasing from less to more hydrodynamic conditions (either high current speed or wave action, second axis), may provide a similar explanation.

Furthermore, functional evenness (functional complementarity, opposed to redundancy) exhibited opposite trends along the first RLQ axes. Over the whole area, its increase toward *A*-conditions, like functional dispersion, was likely due to an increase in density in *A*-strategists among *r*- and *K*-strategists, complementarily filling the functional community space. In contrast, the reverse trend in the high-dynamics habitat was likely due to the omnipresence of *A*-strategists across the seascape and the functional diversifications in *r*- and *K*-environments on the left side of the first axis where larger *r*- and *K*-abundances balance the functional distribution. In the low-dynamics habitat, given the presence of *A*-strategists limited to the margins of the area (Fig. S3), the same reverse trend might be explained by additional processes. There, the presence of engineer species (e.g. *Callianassa subterranea*, *Chaetopterus variopedatus*, *Upogebia deltaura*) might facilitate

space occupation across the sediment matrix by burrowing, sediment mixing and bioirrigation (Pearson 2001, Kristensen et al. 2012), benefiting various species as supported by higher functional richness. While we focussed on environmental forces that impact response traits (expressing fitness), further analyses based on effect traits would provide interesting insights on the contribution of ecological engineering to this functional filling (Snelgrove 1999, Hewitt et al. 2008, Thakur & Wright 2017).

4.4. Scale and seascape geomorphological implications

The Dutch sector of the North Sea displays geomorphological variations strongly associated with large-scale ecological variations in the whole-area pattern (first RLQ axis), as indicated by large-scale BPIs. However, the expression of these BPIs was limited to the major latitudinal depth gradient that segregated the 2 main habitats, and associations between small-scale geomorphology and small-scale ecological variations could not be clearly detected, even in the presence of prominent geomorphological contrasts in the southern area. As a result, only 2 extreme benthic functional types were grossly detected in association with shallow high dynamics (*A*-strategy) and deep low dynamics (indistinctly *r*- and *K*-strategies). The importance of large-scale BPIs in the low-dynamics pattern was more expectable given the smoother bed morphology. There, the small-scale ecological variations could only be attributed to the slightly variable hydrology and sediment characteristics. Although the spatial resolution of the bathymetric data may have been too limited to get significant relationships with small-scale BPIs, the second BPI-PCA axis supported the association between geomorphology and life strategies in high dynamics. *A*-selected communities occurred mainly on convexities of high curvature, generally associated with higher turbulences, whereas *r*- and *K*-communities could occur in troughs, depending on slope. This pattern is corroborated by a recent small-scale study focussing on macrobenthic assemblage composition along asymmetrical sand waves (200 m long) in the highly dynamic part of the present study (Cheng et al. 2021), showing taxa typical of *A*-strategy dominating the most turbulent parts (gentle slopes and crests), whereas assemblages of other various taxa were found in the less turbulent parts (steep slopes and troughs). From the whole area to the high-dynamics patterns, the decorrelation between depth

and current speed and wave energy seems to be the major explanation for the higher benthic functional complexity in high dynamics. By generating local independent changes in hydrological and sediment conditions, alternation of bed forms was the major source of small-scale ecological variations, blurred over larger scales by other types of contrasts like those in low dynamics.

In the present study, these findings reveal a spatial scale-dependence whereby the detection of all 3 life strategies depends on greater seascape heterogeneity, more locally pronounced. In this respect, our second hypothesis was supported. However, the spatial extent considered in this study does not enable us to define a universal scale at which the most divergent life strategies can be detected given the possible independence between extents of sand wave fields or sand banks and continental shelf surface area. At the least, these findings advocate for multiple applications to shed light on this point given the contingent nature of ecosystems (Belyea & Lancaster 1999, Peres-Neto et al. 2012).

4.5. Conclusions

In this study, we provided field evidence of evolutionary trait convergences in the benthos from a soft-sediment shelf, as expected through environmental filtering. However, we also showed that the likelihood of the process may not be greater at larger spatial scales as usually expected (Weiher & Keddy 1995), but may depend on spatial contingencies of habitat heterogeneity (Peres-Neto et al. 2012), with variable assembly patterns across changing scales and associated heterogeneities. Nevertheless, and contrary to current opinions (Aguilar-Trigueros et al. 2017), we showed that environmental filtering is not a relic in the marine benthos where life strategies can be clearly determined by physical forces, although we do not neglect implications of ecological engineering at smaller scales as another assembly rule; further investigations on effect traits could shed light on this point. As reflected in the outcomes of this work, the use of life strategies provides a synthetic way of interpreting species community patterns and more considerations of the concept could facilitate comparisons between studies and exchanges between benthic ecologists through a common language beyond biogeographic differences (Weiher & Keddy 1995).

Soft-sediment shelves are distributed worldwide (Harris & Baker 2020), and the immutable properties of hydrological effects on sediments may shape uni-

versal patterns of benthic synecological organisation in these marine systems, since the deterministic nature of assembly rules remains universal (Belyea & Lancaster 1999). Although ecosystems may be subject to spatial contingencies, assembly rules in soft sediment shelves might generally operate in the range of spatial scales identified in the present study, while disappearing at larger scales. In spite of the negative effects of physical forces on taxonomic diversity, hydrodynamics generate environmental characteristics that remain sufficiently contrasted to maintain a mosaic of heterogeneous benthic functioning with specific assembly rules beyond simple taxonomic counts.

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