Marine Environmental Research 201 (2024) 106712

Contents lists available at ScienceDirect

Marine Environmental Research

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

Environmental influence on the functional ecological structure of benthic macrofaunal communities of the northwest Iberian coast

Catarina M. Alves [a,b,*], Marisa A. Gomes [a,b], Jesus S. Troncoso [b], Pedro T. Gomes [a]

[a] Centre of Molecular and Environmental Biology, Department of Biology, Campus de Gualtar, University of Minho, 4710-057, Braga, Portugal
[b] ECOCOST Lab, Marine Research Centre (CIM-UVIGO), Department of Ecology and Animal Biology University of Vigo, 36310, Vigo, Spain

ARTICLE INFO

Keywords:
Functional diversity
Biological trait analysis
Benthic macrofaunal communities
Artificial substrates
Northwest Iberian coast

ABSTRACT

Evaluating the functional structure of benthic macrofaunal communities provides insights into how environmental drivers shape the ecosystem and establishes a baseline knowledge of the communities' dynamics and functioning. This understanding allows the prediction of responses to environmental changes and the implementation of efficient conservation and management strategies. Here we examine the structures and functions of benthic macrofaunal communities on the Northwest Iberian coast concerning environmental factors such as depth, hydrodynamic energy, and bottom type. The results suggest that the community assemblages and their function are structured by factors which influence food availability and habitat heterogeneity. The different sites exhibited different trait compositions and functional structures, indicating that distinct functions are performed according to environmental conditions. The communities found in sandy bottom areas with low hydrodynamic conditions presented frail functionality and demonstrated high vulnerability to alterations in their environment. Conversely, the communities found in rocky bottoms with high hydrodynamic conditions exhibited a fulfilled functional niche space, rendering them more resilient to such changes and less prone to loss of function. Although the analyses did not reveal significant differences in the factor depth, its influence on several factors seems relevant in shaping the functional structure of the communities. These findings highlight the importance of understanding the impact of local environmental conditions on ecosystem functioning, to effectively implement monitoring, management, and conservation strategies.

1. Introduction

Marine environments and their associated biodiversity hold unique inherent worth, providing critical ecosystem services such as regulatory systems, food, energy, and habitat. Preserving these elements becomes essential to maintaining the structure and functioning of numerous ecosystems and the health of global populations (Alsterberg et al., 2017; Lotze, 2021; Ward et al., 2022). The marine ecosystem of the NW Iberian coast is of particular relevance due to its unique conditions. This region possesses strong latitudinal environmental gradients and is strongly influenced by upwelling events (Gomez-Gesteira et al., 2011; Pardo et al., 2021). These phenomena directly affect the primary production, the thermohaline properties (temperature and salinity), and species distribution. The NW Iberian coast, as the northern boundary of a broader upwelling system's influence (Eastern North Atlantic Upwelling System), is characterised by high primary production proving to have great economic and social value (Gomez-Gesteira et al., 2011; Ríos et al., 1992; Torres and Barton, 2006). According to recent studies, the NW Iberian coast is estimated to be one of the regions most affected by climate change (Bakun et al., 2015; Pardo et al., 2021; Sousa et al., 2019). Climate changes will modify the NW Iberian Coast's oceanographic properties, intensifying local winds and promoting surface heating (Pardo et al., 2021; Sousa et al., 2019). This prompts an urgent description of the distribution patterns within this regional environment, to successfully characterise local processes and understand the influence of environmental conditions.

Understanding patterns within community composition, both in terms of taxonomic and functional diversity, as well as their response to environmental changes, provides important information for developing effective strategies for conservation and ecosystem management (Saeedi et al., 2022; Tyler and Kowalewski, 2018). Benthic macrofaunal assemblages, key components of shallow marine ecosystems, are great

* Corresponding author. Centre of Molecular and Environmental Biology, Department of Biology, Campus de Gualtar, University of Minho, 4710-057, Braga, Portugal.
E-mail address: catarinamacedoalves@gmail.com (C.M. Alves).

https://doi.org/10.1016/j.marenvres.2024.106712
Received 20 June 2024; Received in revised form 16 August 2024; Accepted 26 August 2024
Available online 28 August 2024

indicators of environmental conditions and environmental changes (Borja et al., 2000; Breine et al., 2018; Sun et al., 2021). These organisms have sedentary habits, long lifespans, and high diversity, making them valuable bio-indicators for monitoring a wide range of environmental disturbances (Han et al., 2021; Patrício et al., 2012; Piló et al., 2015). They play an important role in detritus decomposition, nutrient cycling, and energy transfer to upper trophic levels (Xu et al., 2018). Moreover, their diverse feeding modes (e.g., carnivory, detritivore, or filter feeding) and life-history strategies (e.g., free-living, sedentary, or tube building) can be affected by habitat characteristics or environmental conditions (Momota, 2021) which may influence the overall functioning of the ecosystem (Han et al., 2021; Nunes et al., 2008). Therefore, variability in environmental conditions can have varying effects on the balance of ecosystem functions. Traditionally, benthic macrofaunal communities have been used to assess and evaluate the impact of environmental factors on several different environments within shallow marine ecosystems. Some of the most explored are the benthic communities of the intertidal shores (Alves, 2017; Boaventura et al., 2002), the soft-sediment bottoms (Lourido et al., 2010; Piló et al., 2015; Veiga et al., 2016, 2017) and the estuary or inlet environments (Alves et al., 2024a; Nunes et al., 2008; Patrício et al., 2012; Pinto et al., 2009). Within a functional framework, a few studies have been implemented analysing environmental variations (Alves et al., 2024b; Llanos et al., 2020; Momota, 2021; Sivadas et al., 2020; Törnroos et al., 2013; Van Der Linden et al., 2012; Weigel et al., 2016). Despite these efforts, the complex dynamics that govern subtidal benthic macrofaunal communities persist as an essential question, which would help to understand the intricate relationships between certain environmental factors (e.g. depth, light intensity, hydrodynamics) and the benthic macrofaunal organisms taxonomic and functional characteristics (Kraufvelin et al., 2011; Paz-Ríos et al., 2020; Tyler and Kowalewski, 2018). Physical elements like depth and bottom type are believed to be influential in structuring macrofaunal communities (Coleman et al., 2007; Paz-Ríos et al., 2020). Depth variations lead to alterations in light availability, turbulence, and hydrodynamics (Denny, 2006; Wilkinson and Evans, 1989). Consequently, these factors can also influence sedimentation patterns (Airoldi and Cinelli, 1997) and the fluxes of propagules and nutrients (Bertness et al., 1992; Montes et al., 2021). This evaluation of marine environments and characteristics is a complex and substantial undertaking, leaving some matters unsuccessfully explored.

In this study, we analyse the spatial variability of the subtidal macrofaunal community on the NW Iberian coast considering environmental factors such as depth, hydrodynamic energy, and bottom type, using functional analysis and standardised sampling methods. Functional diversity is recognised as a powerful and complex predictor of ecosystem functioning (Cadotte et al., 2011; Griffin et al., 2009; Petchey and Gaston, 2006), which in contrast to traditional measures, operates under the premise of a mechanistic link between diversity and the ecological phenomena under investigation (Cadotte et al., 2011). This approach allows us to comprehend the mechanisms and circumstances shaping communities leading to a gradual integration of functional and standardised methodologies into traditional ecological studies.

This study aimed to i) identify and describe the functional composition and distribution of macroinvertebrates associated with complex habitats along the highly dynamic NW Iberian coast, and ii) to analyse the influence of the environmental conditions (water depth and bottom type) in the functional distribution and composition of the subtidal macrofaunal community of NW Iberian coast. Despite numerous research efforts dedicated to investigating the associated fauna and their distribution, this represents the first application of BTA in this region, which allows the establishment of a direct connection between the environmental processes and the ecological functioning of the ecosystem. The traits applied address the capacity to detect changes in environmental conditions with traits reflecting production, decomposition, elemental cycling, and vulnerability or resistance/resilience. This study's strength lies in its ability to identify and analyse the specific changes in the functional composition of the ecosystem, and how these changes affect its overall functioning.

2. Material and methods

2.1. Study site

This study was conducted between June and September 2022 on the coast of Viana do Castelo at 41.7°N 8.8 W. This coastal region is characterised by a significant absence of natural barriers, which makes it very susceptible to the direct effects of coastal processes (Gomes et al., 2024; Rosa-Santos et al., 2009). The region is affected by a dominant NW-W swell and by a semi-diurnal tidal regime, with the largest spring tides of 3.5–4.0 m. (Rubal et al., 2021; P. Veiga et al., 2013). Prevailing winds arrive from the north, facilitating nutrient enrichment and increasing biological production in spring and summer. Conversely, during the year's remaining months, the winds shift to a southerly direction, promoting the influx of superficial coastal waters (McClain et al., 1986; Rosón et al., 2008; Wooster et al., 1976). These dynamics have a significant influence on various sedimentary processes, local thermohaline properties and local primary production (Torres and Barton, 2006).

The subtidal geomorphology of this region is characterised by a complex combination of rocky reef systems, pebble bottoms and soft sandy bottoms (Dias et al., 2002b; Martins et al., 2007; Vitorino et al., 2002). This heterogeneity creates a highly complex seafloor which generates contrasting environmental conditions within close distances. In the NW Iberian continental shelf, the highly energetic hydrodynamic conditions lead to sediment remobilisation of sandy deposits and the covering of broad areas of this region (Dias et al., 2002a).

The rock bottom areas are usually affected by high-hydrodynamic energy and therefore exhibit considerable low sediment deposition. On the other hand, the sandy bottom areas are usually affected by low-hydrodynamic energy which allows for high sediment deposition. This dynamic of conditions is the basis for the analysis of factors such as water depth, bottom type, and hydrodynamic energy. Each factor allows the analysis of two categories. Two sites (S2 and S3) were located within a rocky reef area with two different depths (S3: <12 and S2: 26 m), while the other two sites (S1 and S4) were located within a sandy bottom area also at two different depths (S4: <12 and S1: 26 m). The rocky reef sites (S2 and S3) correspond to high hydrodynamic energy areas and the sandy sites (S1 and S4) correspond to lower hydrodynamic energy areas (Fig. 1).

2.2. Study design and sampling methodology

Once the study design was established, artificial substrates (AS) mimicking a 3D complex habitat were created and deployed at the four sites. These substrates were anchored on the seafloor by scuba divers. The estimated surface space available for colonisation, calculated with ImageJ analysis software after the digitalisation of the structures, is around 950 cm^2 (Rasband, 1997) (Fig. 2). This methodology was created to avoid destructive sampling effectively, garnering recognition as a valid, replicable, standardised alternative tool for monitoring studies (Alves et al., 2024a; Alves et al., 2024b; Carreira-Flores et al., 2020). Nonetheless, it is important to interpret the ecological results obtained when using this methodology with caution, as it presents particular dynamics of colonisation and succession (Sokołowski et al., 2017).

Samplings occurred in September 2022, where four replicates were collected at each location. The collection process, conducted by scuba diving, involves placing each substrate meticulously in a 0.5 μm mesh bag before removing it from the anchoring system. This process is carefully done to avoid any loss of allusive organisms. The macrofauna is then sorted from the AS with washings through a 0.5 μm mesh sieve and later stored in an ethanol solution at 4 °C. In a second sorting process, the macrofauna is once again separated from the associated biological

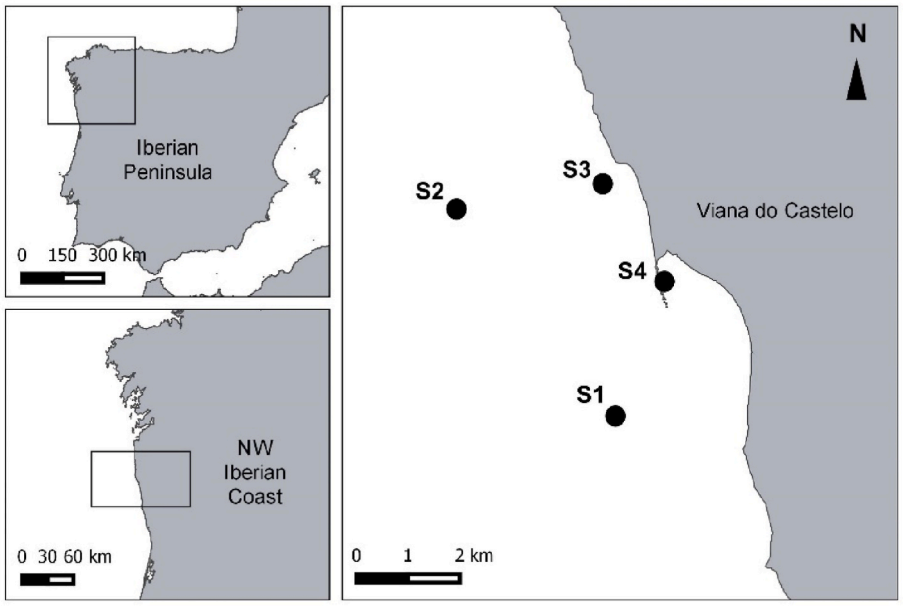

Fig. 1. Viana do Castelo, northwest coast of the Iberian Peninsula (41.7°N 8.8 W). Sampling locations are distributed along the coast (S1- site 1, S2 – site 2, S3 – site 3, S4 – site 4).

Fig. 2. Artificial substrate developed to simulate a 3D complex habitat. The top part mimics complex macroalgae and the bags mimic crevices and fissures environments.

material and organized according to their respective orders for later identification until the species level. The identification process was carried out using a binocular microscope, with the support of taxonomic identification manuals and keys (Hayward and Ryland, 1995; Lincoln, 1979; Naylor, 1972; Saldanha, 1995; Wirtz and Debelius, 2003) as well as support from recognised specialists in several taxa.

2.3. Trait selection and values

The identified species were classified into 8 distinct functional traits and 43 categories (Table 1). These categories capture the essential functions of macrofaunal communities within this coastal ecosystem. The selection process for these traits was carefully made based on the capacity to detect changes in environmental conditions (including traits reflecting production, decomposition, elemental cycling and vulnerability or resistance/resilience) and the quality of the data available. The decisions regarding the selection of traits, the modality divisions and which traits were linked to key mechanisms and functions were based on the existing literature (Bremner et al., 2006a,b; Frid et al., 2008; Törnroos and Bonsdorff, 2012; Beauchard et al., 2017; Dissanayake et al., 2018; Lam-Gordillo et al., 2020) and on BIOTIC - Biological Traits Information Catalogue.

The acquisition of trait information relied mostly on a variety of published literature (Hessler, 1981; Hily and Bouteille, 1999; Ruppert et al., 2004; Gaudêncio and Cabral, 2007; Navarro-Barranco et al., 2013; Queirós et al., 2013; Jumars et al., 2015; Quell et al., 2021; David S. Clare et al., 2022) as well as on online information databases (Encyclopedia of Life, 2023; Marine Life Information Network, 2023; PolyTraits, 2023; World Register of Marine Species, 2023; Palomares and Pauly, 2023). In instances where specific or reliable information was unavailable, genus- and family-level information was used.

Each species was assigned a 'binary' code to indicate its association with specific biological trait categories. The score 0 denotes no affinity to a trait category, while the score 1 indicates affinity towards a particular trait category. This coding method ensures a consistent data structure and reduces the likelihood of errors in data entry and analysis, although it is important to acknowledge the potential reduction in the complexity of affinities levels.

2.4. Data analysis

The taxonomic analysis of the communities in the study involved the calculation of several descriptive parameters. Species richness (S) (Hurlbert, 1971), Shannon-Winner index (H') (Shannon, 1948), Simpson dominance index (D) (Simpson, 1949), and Pielou evenness index (J') (Pielou, 1966) were calculated based on the abundance of individuals per site. For the functional analysis of the communities in the study the parameters functional richness (FRic) (Mason et al., 2005; Mouchet et al., 2010; Villéger et al., 2008), functional dispersion (FDis) (Laliberte and Legendre, 2010) and Rao's quadratic entropy (RaoQ) (Champely and Chessel, 2002; Mouchet et al., 2010; Rao, 1982) were calculated as estimators of functional diversity, while functional evenness (FEve) (Mason et al., 2005; Mouchet et al., 2010; Villéger et al., 2008), functional divergence (FDiv) (Mason et al., 2005; Mouchet et al., 2010;

Table 1
List of included functional traits (8), trait categories (43), key mechanisms and functions.

Trait	Category	Acronym	Key Mechanism of functions	Function	Effect	Response
Feeding Mode[b]	Active suspension Passive suspension Subsurface deposit Surface deposit Predator Scavenger Carnivore Grazer Detritivore Parasite	SusA SusP DepSs DepS Pred Scan Carn Graz Detri Par	Transport from pelagos, Transport within sediment, Facilitation/provision of material, Energy fixation/rate of transfer.	Elemental cycling (within benthos & benthos-pelagos). Production, Food/Resources.	x	x
Habit[b]	Burrow dwelling Crevices/holes Epi-endobiotic Free-living Tubicolous Permanent attachment Temporary attachment	BurD Crev EpiE FreL Tub AttP AttT	Ability to perform transport and extent. Turnover. OM decomposition. Biogenic habitat creation.	Elemental cycling (within benthos & benthos-pelagos).	x	x
Larval development[b]	Benthic direct Pelagic lecithotrophic Pelagic planktotrophic	BDir PLec PPla	Proxy for recruitment. Success. Food for predators. Resilience.	Elemental transport, Production. Temporal pattern.		x
Sensitivity to disturbance (AMBI)[a]	Very sensitive Indifferent Tolerant 2nd order opportunist 1st order opportunist	GSen GInd GTol G2oO G1oO	Vulnerability or resistance/resilience of a species towards pollution or climate change induced changes in water biogeochemistry.	Temporal pattern.		x
Lifespan[b]	Less 1 year 1–3 years 3–10 years More 10 years	Lu1 L1.3 L3.10 Lo10	Energy fixation, Turnover, production rate. Food for predators. OM decomposition	Production, Elemental cycling.		x
Body Size[b]	Under 10 mm 11–20 mm 21–100 mm 101–200 mm 201–500 mm More 500 mm	Su10 S11.20 S21.100 S101.200 S201.500 So500	Rate of production, amount of exchange, facilitation. Competitive effect. Turnover. OM decomposition.	Production, Elemental cycling, Food/ Resources.	x	x
Mobility[b]	Swimmer Burrower Crawler/Creep Sessile	Swi Burr Craw Sess	Turnover, Transport, Facilitation of materials. Response to competition. OM decomposition.	Production, Elemental cycling (pelagos-benthos & within benthos), Food/Resources, Temporal pattern.		x
Egg development[b]	Assexual Sexual benthic Sexual brooded Sexual pelagic	Ass SBen SBro SPel	Proxy for recruitment. Success. Resilience.	Elemental transport, Production Temporal pattern.		x

[a] Discrete trait (species can only express one modality of the trait).
[b] Combinatory trait (species can be assigned to one, several, or all of the modalities in the trait).

Villéger et al., 2008) and functional redundancy (FRed) (Van Der Linden et al., 2012) were calculated as estimators of species distribution within the trait space. These indices were calculated in the 'fundiv' package (Bartomeus, 2015), which includes the FD indexes (Petchey et al., 2004) and the 'FD' package (Laliberté et al., 2014). To test the evolution of these indices with the factors, General Linear Mixed Models were applied, based on a two-way model design with three factors: water depth (fixed, two levels: 26 m deep vs < 12 m deep), bottom type (fixed, two levels: rocky bottom vs sandy bottom), and site nested in depth (random four levels: site 1 vs site 2 vs site 3 vs site 4) with 'lme4' library (Bates et al., 2015). A correlation analysis was used to analyse the relationship between the taxonomic diversity indices (S, J′, H′, D) and the functional diversity indexes (FRic, FDis, FEve, FDiv, and FRed), via the 'Hmisc' package (Harrell Jr and Dupont, 2023). To evaluate shifts in trait composition and expression, the functional identity was calculated as community-level weighted means of trait category expressions (CWM), using the BAT package (Cardoso et al., 2022). All previous steps were performed using the statistical computing software R ver. 4.2.2. Utilizing PRIMER 6.0 software, community analyses were performed using a non-parametric permutational multivariate analysis of variance (PERMANOVA). The test design was based on the same two-way model with two factors water depth (fixed, two levels: 26 m deep vs < 12 m deep) and site nested in depth (random four levels: site 1 vs site 2 vs site 3 vs site 4) to uncover if any of the factors or their interaction affected the CWM. Afterwards, a PERMDISP procedure was conducted to test whether the observed differences were attributable to distinct multivariate dispersion in the centroid's location (Anderson, 2017). A pair-wise test was also conducted to assess the variation in the trait expression within each factor between depths and sites. Additionally, a non-metric multidimensional scaling (nMDS) was performed to analyse the responses of the assemblages based on the Bray-Curtis dissimilarity matrix. This enables the visualisation of the dissimilarity patterns among

the assemblages. When significant differences in functional composition were detected, a similarity percentage analysis (SIMPER) was applied, with a 70% accumulative contribution cut-off. This analysis allows us to emphasise the traits responsible for the significant observed differences in the community.

3. Results

3.1. Benthic macrofaunal assemblage structure

A total of 136 taxa were found across the four sampled sites (S1, S2, S3, and S4). The species richness within the sampled sites ranged from 34 to 69 species, while total abundance varied from 378 to 3786 individuals. The RaoQ, as well as FDis within the benthic macrofaunal communities, showed that site 2 had higher values (Fig. 3A and D), while FRic displayed higher values in the sites with rocky bottoms (S2 and S3) (Fig. 3B). FDiv (Fig. 3C) reveals a high variation within the sites, showing differences between rocky bottom sites and sandy bottom sites and between depths. The FEve displayed no significant pattern, with site 4 having the highest values (Fig. 3E.). FRed revealed a clear increasing pattern with the decrease of depth. The Generalised Linear Mixed Model performed on the indices revealed significant differences for the factor 'depth' in FDiv and FRed and for the factor 'bottom type' in FRic and FDiv (Table A1).

The Pearson correlation analysis results indicated that FRic and RaoQ did not have significant correlations with species diversity. However, FRic was significantly correlated with S. Additionally, FDiv was negatively correlated with FRed, while FRed showed positive correlations with H′, D, and J' (Table 2).

3.2. Responses in the functional structure

The PERMANOVA results indicated that the community-weighted means of trait expression (CWM) did not significantly differ for the factor depth (P = 0.1671). However, significant differences were observed for the factor of site (P = 0.0001). PERMDISP was run to test the homogeneity of multivariate dispersions. The overall tests comparing the sites were not statistically significant (P (perm) = 0.713), meaning that the dispersion of the replicates does not influence the differences between the sites (Table 3). The individual pair-wise test showed significant differences between sites 1 and 2 within 'depth 26', and between sites 3 and 4 within 'depth 12' (Table 4).

The nMDS ordination showed a separation of macroinvertebrate assemblages according to different sites (Fig. 4). The groups are formed according to the distribution of community-weighted means of trait expression, where site 1 forms a differentiated group.

3.3. Trait contribution across factors

SIMPER analyses have been performed to identify which traits and categories most contributed to the observed differences in CWM. The total percentage of category contribution within each trait, as well as the single categories, highlight the most important traits regarding the factors in the analysis. This analysis revealed that 18 categories accounted for most differences between Sites 1 and 2 (Table 5). These categories contributed more than 70% to the total dissimilarity, with 12

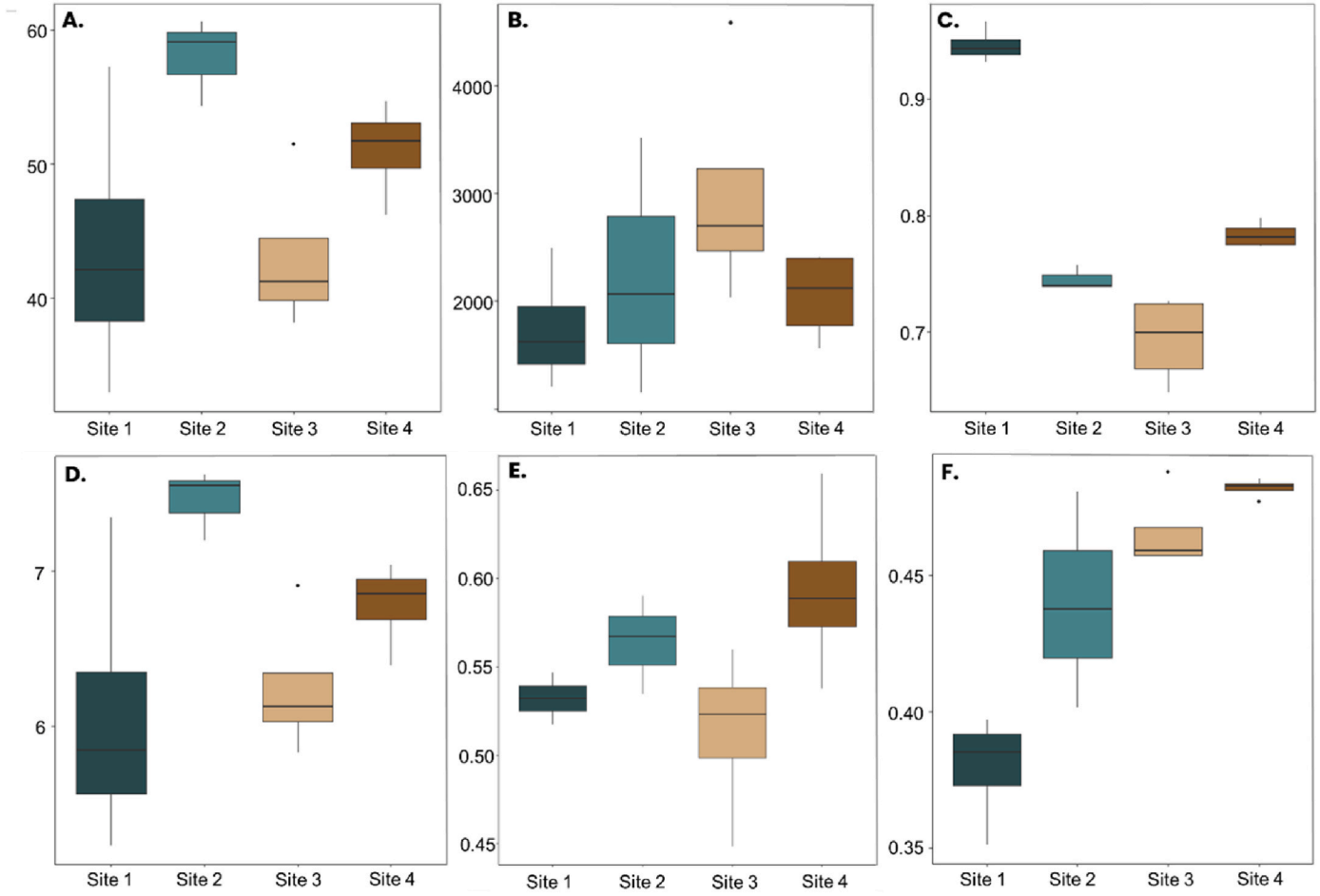

Fig. 3. Box-plots of A. Rao's quadratic entropy (RaoQ), B. functional richness (FRic), C. functional divergence (FDiv), D. functional dispersion (FDis), E. functional evenness (FEve) and F. functional redundancy (FRed) through the sampled sites. Sites 1 and 2 are in depths of 26 m, and sites 3 and 4 are located in depths <12 m.

Table 2
Results of correlation analysis between the benthic macrofaunal communities functional indices (FRic – Functional Richness; FDis – Functional Dispersion; FEve – Functional Evenness; FDiv – Functional Divergence; and FRed – Functional Redundancy) and species diversity (S – species number; J′- Evenness, H′- Shannon-Wiener index; D - Simpson dominance index).

	FRic	FDis	FEve	FDiv	RaoQ	*FRed*	*J'*	*H'*	*D*
FRic									
FDis	−0.067								
FEve	−0.274	0.498							
FDiv	−0.554	−0.274	0.066						
RaoQ	−0.112	0.989[b]	0.557	−0.155					
Fred	0.562	0.170	0.225	−0.770[a]	0.119				
J'	0.245	0.473	0.497	−0.673	0.434	0.896[b]			
H'	0.379	0.399	0.432	−0.706	0.356	0.948[b]	0.982[b]		
D	0.413	0.395	0.401	−0.744	0.347	0.961[b]	0.972[b]	0.995[b]	
S	0.772[a]	−0.356	−0.328	−0.330	−0.386	0.430	0.051	0.238	0.266

[a] Significant at 0.05 level.
[b] Significant at < 0.001 level.

Table 3
Permutational multivariate analysis of variance (PERMANOVA) results of community-weighted means of trait expression (CWM). Bold values highlight statistical significance.

Source	*df*	SS	MS	Pseudo-F	P (perm)	Unique terms	P (MC)
Depth	1	1734.6	1734.6	2.811	0.1671	6	0.1669
Site (Depth)	2	1241.2	620.58	24.099	**0.0001**	9937	**0.0001**
Residuals	11	283.27	25.752				
Total	14	3481.2					
PERMDISP (Depth)	**F: 51.98**				**P(perm): 0.001**		
PERMDISP (Site)	**F: 0.981**				**P(perm): 0.713**		

Table 4
Results of pairwise tests of community-weighted means of trait expression (CWM) between site nested in depth.

Groups	t	P (perm)	Unique Perms	P (MC)
Depth 26: S1 vs S2	4.9353	**0.0302**	35	0.001
Depth 12: S3 vs S4	4.5001	**0.0281**	35	0.0008

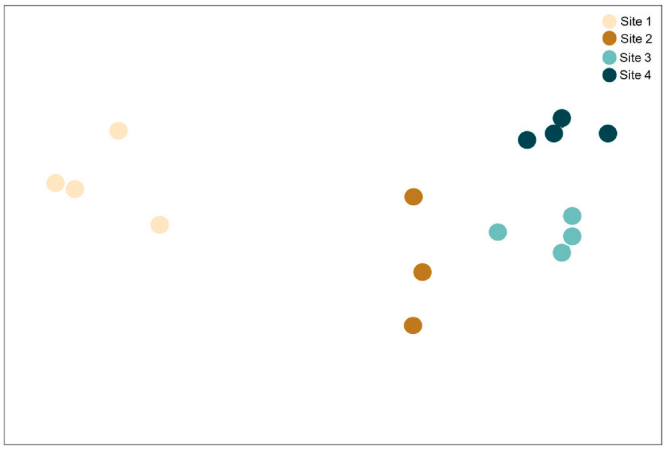

Fig. 4. Non-metric multidimensional scaling (nMDS) ordination based on Bray–Curtis dissimilarity of centroids (calculated in four different sites). (a) Site 1: beige (S1); (b) Site 2: Brown (S2), (c) Site 3: light blue (S3) Site 4: dark green (S4).

of the categories contributing with values > 3%. Within Habit and Mobility, the expression of categories 'free-living', 'permanent attachment', and 'sessile' had the most significant and consistent contributions to the dissimilarity between S1 and S2 (δi = 0.0129, δi% = 7.3604, δi/SD = 6.816; δi = 0.0127, δi% = 7.212, δi/SD = 5.73; δi = 0.0126, δi% = 7.1645, δi/SD = 5.781). Within Egg development and Habit the categories 'sexual benthic' (δi/SD: 1.934) and 'Epi-endobiotic' (δi/SD: 2.013) reveal the lowest δi/SD ratios suggesting more variability in their contributions. Site 1 seems to be more associated with trait categories such as 'sessile', 'permanent and temporary attachment', and 'over 10 years', while Site 2 seems to be more associated with 'free-living', 'surface deposit' and '101–200 mm' categories.

This analysis revealed that 19 categories accounted for most differences between Sites 3 and 4 (Table 6). These categories contributed more than 70% to the total dissimilarity, with 9 of the categories contributing with values > 3%. Within Sensitivity to disturbance, Egg development and Feeding mode the expression of categories 'tolerant to disturbance', 'sexual benthic', 'carnivore' and 'active suspension' had the most significant contributions (δi = 0.0071, δi% = 8.2466; δi = 0.0063, δi % = 7.3495; δi = 0.0055, δi% = 6.4092). The most consistent contributors are the categories 'herbivore' (δi/SD = 8.417), 'omnivore' (δi/SD = 6.291) and 'tolerant' (δi/SD = 5.557). Within Lifespan and Habit the categories 'over 10 years' (δi/SD: 1.680) and 'tubiculous' (δi/SD: 1.916) reveal the lowest δi/SD ratios suggesting more variability in their contributions. Site 3 seems to be more associated with trait categories such as 'active and passive suspension feed', 'very sensitive', and 'swimmer'. In contrast, site 4 seems to be more associated with 'tolerant', 'sexual benthic' and 'carnivore' categories.

Community-weighted means (CWM) of trait-modalities expression was plotted to visualise the trait composition for each site (Fig. 5). The dominating trait categories in the benthic macrofaunal communities on the Northwest Iberian coast varied between the sites which represent different environmental conditions. At site 1, the dominating trait categories were 'pelagic planktotrophic', 'sensitive to disturbance', '11–20 mm' and 'suspension feed'. At site 2, were 'crawler', 'pelagic planktotrophic', 'sensitive to disturbance', 'free-living', and '3–10 years'. At site 3, were 'crawler', 'sensitive to disturbance', 'sexual brooded', '1–3 years', and 'deposit feed'. And at site 4, were 'crawler', 'sexual brooded', 'deposit feed', and 'under 10 mm'.

Table 5
SIMPER analysis results for the top categories contributing to the dissimilarity between Sites 1 and 2. Av.CWM indicates the average community weighted mean of trait expression-value of the factors, Av.Cont δi indicates the average contribution of each trait category to the overall dissimilarity between the groups, Av.Cont δi% indicates the percentage of the total dissimilarity attributed to each trait, SD indicates the standard deviation of the contributions, δi/SD indicates the ratio of the average contribution (δi) to its standard deviation (SD) and Cum % indicates the cumulative percentages of contribution to the dissimilarity (cut-off at 70% cumulative dissimilarity).

Trait	Category	Av.Cont (δi)	Av.Cont δi %	SD	δi/SD	Av.CWM Site 1	Av.CWM Site 2	Cum %
Habit	Free-living	0.0129	7.3604	0.0019	6.816	0.3131	0.8124	0.052
	Permanent Attachment	0.0127	7.212	0.0022	5.730	0.8517	0.3631	0.102
Mobility	Sessile	0.0126	7.1645	0.0022	5.781	0.8524	0.367	0.153
Lifespan	Over 10 years	0.0125	7.1083	0.0023	5.408	0.8603	0.3787	0.203
Habit	Temporary attachment	0.0123	6.9929	0.0022	5.516	0.8545	0.3807	0.252
Feeding mode	Sub-surface deposit	0.0117	6.6602	0.0025	4.682	0.1163	0.5676	0.299
Body Size	201–500 mm	0.0111	6.3132	0.0034	3.310	0.1169	0.5444	0.343
Mobility	Crawler, Creep and Climb	0.0108	6.1661	0.0024	4.543	0.5112	0.9289	0.387
Body Size	101–200 mm	0.0107	6.0724	0.0034	3.151	0.1563	0.5676	0.430
	11–20 mm	0.0087	4.9395	0.0022	3.969	0.8709	0.5366	0.464
Feeding mode	Surface deposit	0.0087	4.9134	0.0027	3.166	0.4470	0.7796	0.499
Lifespan	3–10 years	0.0083	4.7146	0.0035	2.356	0.4664	0.7851	0.532
	1–3 years	0.0065	3.7123	0.0023	2.875	0.2344	0.4865	0.558
Egg development	Sexual benthic	0.0063	3.6038	0.0033	1.934	0.7678	0.5278	0.583
Feeding mode	Predator	0.0063	3.5925	0.0017	3.828	0.2080	0.4519	0.609
Mobility	Swimmer	0.0062	3.5089	0.0027	2.254	0.1975	0.4364	0.633
Feeding mode	Detritivore	0.0059	3.3466	0.0029	2.013	0.3223	0.1532	0.657
Habit	Epi-endobiotic	0.0058	3.3148	0.0034	1.728	0.5208	0.2968	0.680

Table 6
SIMPER analysis results for the top contributors of the dissimilarity between Sites 3 and 4. Av.CWM indicates the average community weighted mean of trait expression-value of the factors, Av.Cont δi indicates the average contribution of each trait category to the overall dissimilarity between the groups, Av.Cont δi% indicates the percentage of the total dissimilarity attributed to each trait, SD indicates the standard deviation of the contributions, δi/SD indicates the ratio of the average contribution (δi) to its standard deviation (SD) and Cum % indicates the cumulative percentages of contribution to the dissimilarity (cut-off at 70% cumulative dissimilarity).

Trait	Category	Av.Cont δi	Av.Cont δi%	SD	δi/SD	Av.CWM Site 3	Av.CWM Site 4	Cum. %
Sensitivity to disturbance	Group III -Tolerant	0.0071	8.2466	0.0013	5.557	0.1932	0.4642	0.058
Egg development	Sexual benthic	0.0063	7.3495	0.0021	2.949	0.2582	0.5000	0.110
Feeding mode	Carnivore	0.0055	6.4092	0.0011	4.919	0.2412	0.4525	0.154
	Active suspension	0.0053	6.1919	0.0009	5.478	0.7582	0.5539	0.198
	Passive suspension	0.0053	6.1593	0.0009	5.526	0.7515	0.5483	0.241
Body Size	201–500 mm	0.0052	6.0646	0.0018	2.842	0.2809	0.0805	0.284
Feeding mode	Scanvanger	0.0048	5.5682	0.0009	4.829	0.3903	0.5740	0.323
Lifespan	Under 1 year	0.0047	5.4936	0.0022	2.172	0.4532	0.6344	0.361
Habit	Tubiculous	0.0045	5.2131	0.0023	1.916	0.4913	0.6627	0.398
Feeding mode	Herbivore	0.0042	4.9106	0.0005	8.417	0.0585	0.2203	0.432
	Predator	0.0042	4.8767	0.0016	2.561	0.5239	0.6847	0.467
Habit	Burrow dwelling	0.0041	4.7634	0.0012	3.533	0.5554	0.3989	0.500
Lifespan	1–3 years	0.0041	4.7400	0.0016	2.593	0.8058	0.6503	0.533
Habit	Temporary attachment	0.0039	4.6092	0.0019	1.994	0.1774	0.3274	0.566
Sensitivity to disturbance	Group I – Very sensitive	0.0038	4.4141	0.0009	4.301	0.9043	0.7591	0.597
Mobility	Swimmer	0.0037	4.2973	0.0017	2.195	0.8223	0.6840	0.627
Feeding mode	Omnivore	0.0034	3.9131	0.0005	6.291	0.1866	0.3154	0.654
Body Size	21–100 mm	0.0029	3.4809	0.0013	2.251	0.4327	0.5470	0.679
Lifespan	Over 10 years	0.0028	3.2986	0.0017	1.680	0.1597	0.2545	0.702

3.4. Spatial distribution of the benthic macrofaunal communities' traits

The trait modality composition revealed several differentiation patterns across the sites. The trait Feeding mode presents a gradient of category distribution with a decrease in depth (Fig. 6A). In this trait within 'depth 26', site 1 has a vast majority of 'suspension feeders' and 'deposit feeders', while site 2 has a more even distribution with 'suspension feeders', 'deposit feeders', 'predator and scavengers' and 'grazer and detritivore'. Within 'depth 12', site 3 has a similar distribution to site 2 with 'suspension feeders' and 'deposit feeders', but with lower numbers for 'grazer and detritivore' and higher for 'predator' and 'scavengers'. Site 4 presents the lowest levels of 'suspension feeders' and the highest levels of 'deposit feeders', 'grazer and detritivore' and 'predator' and 'scavengers'.

The trait Habit reveals an increasing pattern of 'free-living' and 'tubiculous' organisms with a decrease in depth. Site 1 has a high number of 'sessile', 'crevices, holes and under stones' and 'epi-endobiotic' organisms (Fig. 6B). Site 2 on another hand, has a higher number of 'free-living' and 'crevices, holes and under stones' organisms. Sites 3 and 4 present high values of 'free-living', 'burrow dwelling' and 'tubiculous' organisms. The trait modality composition of Lifespan shows that site 1 has a majority of 'more than 10 years' organisms, while site 2 has a higher number of '3–10 years' organisms followed by the categories '1–3 years', and 'more than 10 years' (Fig. 6C). Site 3 has a majority of organisms with '1–3 years' followed by '3–10 years' and 'less than 1 year', while site 4 has a majority of organisms with 'less than 1 year' followed by '1–3 years' and '3–10 years'.

The trait Mobility shows a significantly different pattern for site 1 with a majority of attached organisms while site 2 revealed a majority of 'crawl, creep and climb' organisms followed by 'attached' and

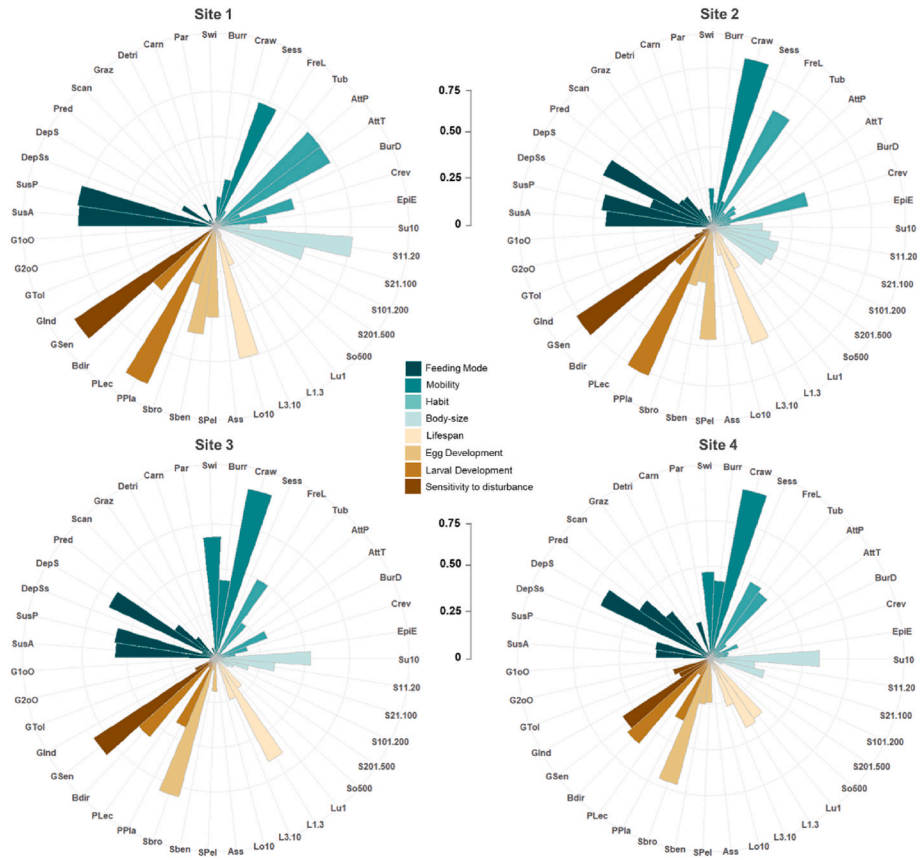

Fig. 5. Community-weighted means (CWM) of trait categories expression of the benthic macrofaunal from four different sites on the Northwest Iberian coast. The scale represents the percentage contribution to CWM. Trait categories labels (acronyms) are defined in Table 1.

'swimmer' organisms. Sites 3 and 4 also exhibited a majority of 'crawl, creep and climb' organisms; however, site 3 exhibited more 'swimmer' organisms and site 4 more 'burrower' organisms (Fig. 6D). The trait Larval development revealed more 'pelagic planktotrophic' organisms in sites 1, 2 and 3, followed by 'benthic direct' organisms (Fig. 7A). Site 4 exhibited a majority of 'benthic direct' organisms followed closely by 'pelagic planktotrophic' organisms. The trait Egg development revealed that site 1 has a majority of 'sexual pelagic' and 'sexual benthic' organisms while site 2 shows a majority of 'sexual pelagic' and 'sexual brooded' organisms. Sites 3 and 4 exhibited a majority of 'sexual brooded' organisms followed by 'sexual pelagic' (Fig. 7B). The trait Body size shows that site 1 has a higher number of organisms '11–20 mm' and '21–100 mm', while site 2 exhibits organisms with '21–100 mm' followed by '101–200 mm', '11–20 mm' and '201–500' mm. Site 3 shows a majority of organisms with '11–20 mm' followed by 'under 10 mm' and '21–100 mm'. Site 4 exhibits a majority of organisms with 'under 10 mm' followed by '21–100 mm' and '11–20 mm' (Fig. 7C). The trait Sensitivity to disturbance reveals that site 1 has the highest number of 'very sensitive' organisms. Sites 2 and 3 also have high values (81.1% and 82.4%), however, they exhibit higher values of 'indifferent' organisms than site 1. Site 4 reveals lower values of 'very sensitive' organisms and higher values of 'tolerant' and 'indifferent' organisms compared to the other sites (Fig. 7D).

4. Discussion

4.1. Patterns of taxonomic and functional measures

The spatial patterns of the macrofaunal benthic communities revealed variations in functional diversity and traits, indicating differences in ecosystem functioning across sites. We identified positive relationships between some taxonomic and functional indices (Table 2). Although taxonomic diversity (D and H′) showed a positive correlation with functional diversity (RaoQ), this correlation was not statistically significant. On the other hand, functional richness (FRic) exhibited a strong and significant correlation with the number of species (*S*′). Similarly, functional redundancy (FRed) revealed a strong correlation with taxonomic diversity (*D*, *H*′) and evenness (*J*′). Numerous studies have documented a range of relationships between taxonomic and functional diversity. Positive relationships have been found (Delfan et al., 2021; Hajializadeh et al., 2020; Lam-Gordillo et al., 2021), but they are not always linear or easy to establish (Wong and Dowd, 2015) and are often subjected to the influence of environmental conditions and habitat heterogeneity (Hewitt et al., 2008; Paganelli et al., 2012; Thrush et al., 2017). This suggests that the assumption of taxonomic diversity as a proxy for functional diversity may not always be suitable and should always be thoroughly investigated. These relationships are complex and yet to be fully understood in several marine ecosystems.

In our study, we also found that some functional measures of benthic communities were site-dependent and varied along environmental conditions (Henseler et al., 2019; Lam-Gordillo et al., 2021; Wong and Dowd, 2015). Rao's quadratic entropy (RaoQ) and functional Dispersion (FDis), both measures of functional diversity, were greater in sites 2 and 4 suggesting a higher expression of traits. This might be explained by the lower values of abundance while still presenting constant functional richness. The sites with rocky bottoms (S2 and S3) exhibited significantly higher functional richness (FRic), which indicates a higher number of traits present in these communities. On the other hand, the sites with sandy bottoms (S1 and S4) presented significantly high functional divergence (FDiv) indicating low resource competition and low niche overlap. Deep sites also (S1 and S2) exhibited high functional divergence (FDiv), suggesting low resource competition and niche

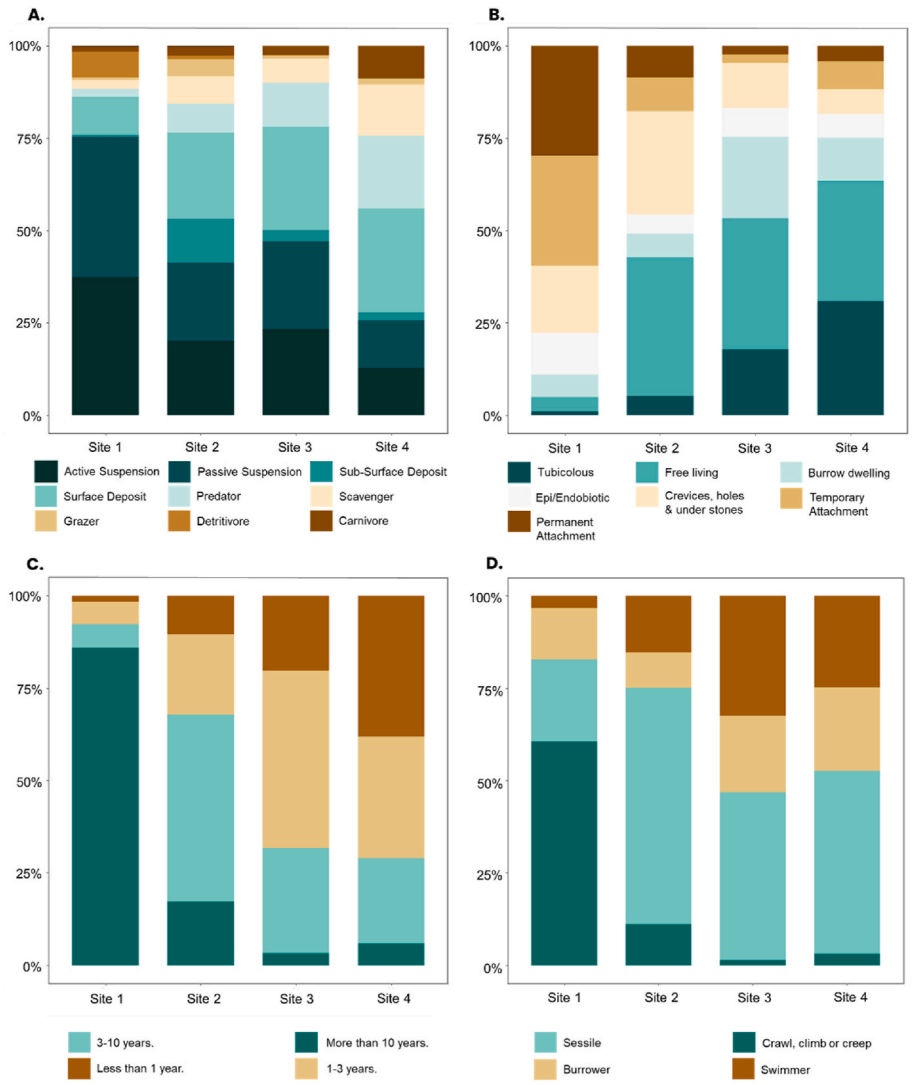

Fig. 6. Traits modality composition for each site (Site 1, Site 2, Site 3, and Site 4). Composition is based on each of the studied traits (A. Feeding mode, B. Habit, C. Lifespan, D. Mobility) for the 136 taxa.

overlap, as well as low functional redundancy (FRed), indicating no overlap of ecological roles. This suggests that the communities from sandy bottom sites have fewer species occupying the available functional niche space and therefore exhibit a frail functionality and heightened vulnerability to alterations in their environment (Díaz and Cabido, 2001; Van Der Linden et al., 2012). Communities from rocky bottom sites, in contrast, have a fulfilled functional niche space, rendering them more resilient to such changes and less prone to loss of function.

4.2. Responses in the functional structure

Multivariate analyses revealed no significant differences regarding the factor depth, while significant differences were found for the factor site (Tables 3 and 4). The functional identity of the communities differed over space, between the communities of sites 1 and 2 and of sites 3 and 4, which is represented in the position of the communities in the multidimensional trait space (Fig. 4). The significance of depth as a structuring agent for macrofaunal communities has long been suggested (Cacabelos et al., 2008; Konar et al., 2009; Lourido et al., 2008; Pirtle et al., 2012; Smale, 2008). However, this notion should not always be assumed as definite, as several variables are involved in the organisation of macrofaunal communities (Alves et al., 2024a). Generally, changes in depth often result in changes in several other factors such as light, degree of disturbance, or sedimentation, thereby expanding the complexity of interactions (Gamito and Furtado, 2009). Alves et al. (2024b) analysed a semi-enclosed bay system in the Northeast Atlantic, examining a range of 4–12 m. The findings revealed that depth only impacted functional richness (FRic), thereby exerting a minimal influence on the overall functionality of the macrofaunal communities. Here, we exerted the range of <12–26 m, in a highly exposed Northwest Iberian coastal environment, revealing significant differences in functional divergence (FDiv) and functional redundancy (FRed), suggesting an influence on the distribution of the multidimensional trait space. Overall, the multivariate analysis revealed no significant differences for the factor depth as in Alves et al., 2024b, but the patterns found for the distribution of the functional niche space should be of notice. The contrast in outcomes might be explained by i) the increase in the range of depths; ii) the increase in the degree of exposition, or iii) a combination of both. This seems to influence the ecological niches occupied by the communities and the potential for replacement in the event of a disturbance, presenting a potential degradation of biodiversity or ecosystem function (Thrush et al., 2003, 2006). The functional development of benthic macrofaunal assemblages cannot be attributed to a single mechanism, as different interacting factors are normally involved (Snelgrove and Butman, 1994; Veiga et al., 2017). It appears that depth

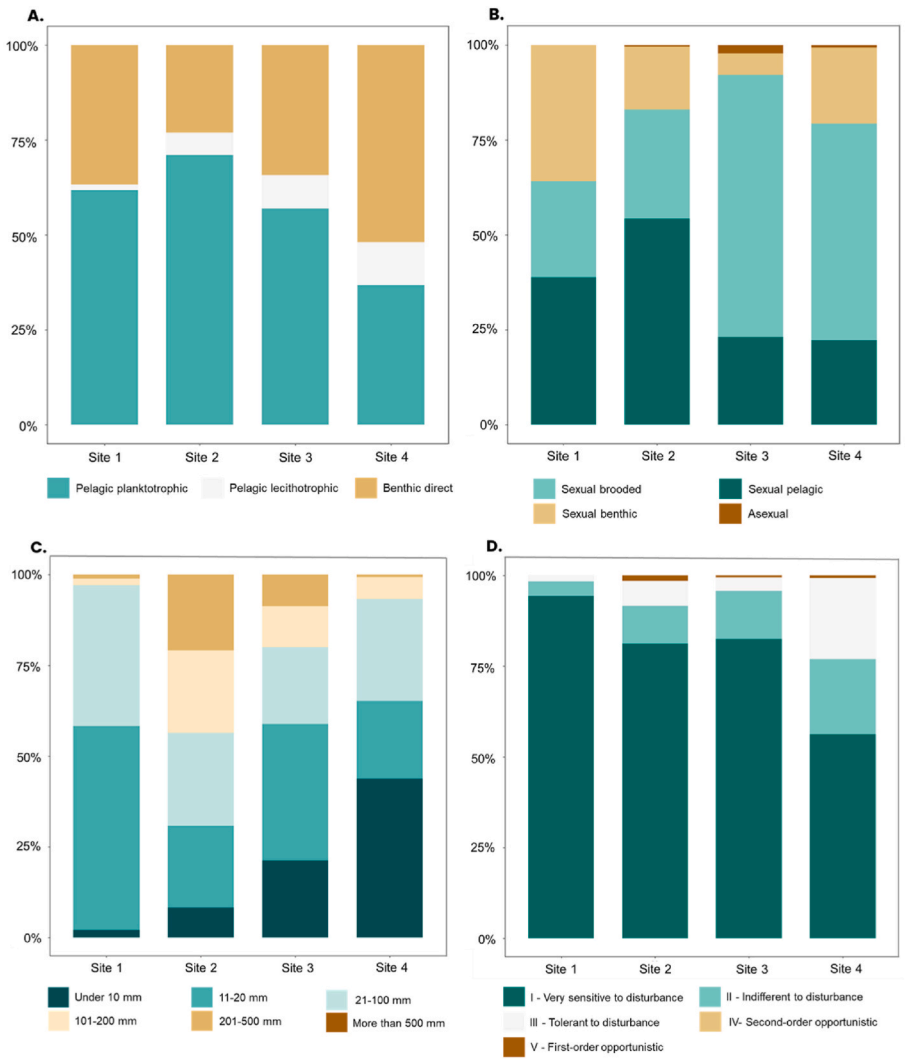

Fig. 7. Traits modality composition for each site (Site 1, Site 2, Site 3, and Site 4). Composition is based on each of the studied traits (A. Larval development, B. Egg development, C. Body size, D. Sensitivity to disturbance) for the 136 taxa.

remains an important structuring agent due to its influence on other factors, such as sediment composition, light availability, hydrodynamics, and bottom type (Gamito and Furtado, 2009; Lourido et al., 2008; Lourido et al., 2008; Pirtle et al., 2012) but alone does not reveal a significant influence. The other factor in the analysis was the site, which exposed significant differences in the functional structure of the communities from sites with different habitats (different bottom types and hydrodynamic energy). This indicates that bottom type and hydrodynamic regime may be relevant factors in shaping the functional structure of the communities as suggested by Noisette et al. (2022); Nowell and Jumars (1984); and van der Wal et al. (2017). Hydrodynamic energy has profound effects on nearly all aspects of an organism's life, such as recruitment and dislodgment of organisms, (Vadas et al., 1990), supply of food and nutrients (McQuaid and Lindsay, 2007), foraging activities of consumers (Taylor and Schiel, 2010; Vergés et al., 2009), physiological activity or modification of their habitat (Noisette et al., 2022). Here, habitats with high hydrodynamic energy tend to be characterised by rock bottoms and high nutrient flows, which leads to highly productive systems dominated by habitat engineer species (macroalgae) that harbour diverse functional benthic macrofaunal communities (Falkenberg et al., 2021; Hurd, 2015). Habitats with lower hydrodynamic energy tend to be characterised by sandy bottoms and lower biological activity due to lower diffusion of nutrients which influences growth rates (Hurd, 2000). In this highly exposed coastal environment of the Northeast Atlantic, the benthic macrofaunal communities appear to be influenced by these physical processes, thus providing a baseline knowledge of potential responses to alterations in the environment.

4.3. *Biological traits analysis across factors*

Through the biological traits analysis (BTA) of the benthic macrofaunal assemblages within the groups exhibiting significant differences, we were able to recognise the traits responsible for these dissimilarities. The top categories contributing to the dissimilarities between sites 1 and 2 were 'free-living', 'permanent attachment' and 'sessile' while between sites 3 and 4 were 'tolerant', 'sexual benthic' and 'carnivore'. This suggests that in the communities living in deep areas, the categories associated with habit and mobility are the most differentiating drivers, while in shallow areas, the most differentiated drivers are the categories associated with disturbances, reproduction and feeding methods (Tables 5 and 6). Upon examination of the primary contributors of dissimilarities associated with the sites, distinct communities emerged. Communities from site 1 were characterised mostly by 'permanent and temporary attachment', 'sessile', 'over 10 years', '11–20 mm', 'sexual benthic', and 'detritivore' organisms. Slower hydrodynamic conditions in combination with higher depths developed sedentary communities with long lifespans. Sessile invertebrates generally dominate in darker and less dynamic conditions, whereas mobile invertebrates dominate in

dynamic areas with high light availability (Blockley and Chapman, 2006; Glasby, 1999; van der Wal et al., 2017). This indicates that sessile invertebrates increase in abundance at higher depths, as light intensity and water motion decline. The presence of a thriving mollusc population in the communities of this site reveals a heightened competition which has resulted in the dominance of larger, long-lived species (Piló et al., 2016). The communities from site 2 were characterised mostly by 'free-living', 'sub-surface deposit', '201–500 mm', 'crawler', '101–200 mm', 'surface deposit', '3–10 years', '1–3 years', 'predator' and 'swimmer' organisms. Here, great hydrodynamic conditions foster the presence of high loads of suspended particles, serving as food for suspension and surface deposit feeders (Lam-Gordillo et al., 2021; Liu et al., 2019; Rand et al., 2018). The importance of food availability has long been recognised as a major structuring factor for benthic communities (Pearson and Rosenberg, 1987; R. Rosenberg, 2001). At depth, it is also common for the proportion of deposit feeders to increase due to the lack of significant impact from wave energy (Dolbeth et al., 2011; van der Wal et al., 2017). These communities, characterised by large, medium/long-lived species with a great variety of feeding methods, require a stable environment without unexpected large changes across time to allow the development of these traits, suggesting environmental quality (Gusmao et al., 2016; Llanos et al., 2020). The deep sites appear to be engaged in providing distinct but quality environments that, due to their differences in physical characteristics, exert a structuring effect on the benthic macrofaunal communities. Ultimately this leads to different functional impacts on the overall ecosystem of the area. The communities of site 3 were characterised by 'active and passive suspension feed', '201–500 mm', 'burrow dwelling', 'sensitive', 'crevices and under stones', '1–3 years', and 'swimmer' organisms. These categories respond to high hydrodynamic conditions and shallow depths, which tend to have high concentrations of suspended particles as food resources for suspension feeders (Lam-Gordillo et al., 2021; Liu et al., 2019; Rand et al., 2018). The category 'burrow dwelling' is normally associated with low hydrodynamic conditions and high organic matter, which contrasts with the conditions found at this particular site (Rutger Rosenberg, 1995). Despite this, it is possible to find certain types of deep burrowing deposit feeders in high-energy areas that are capable of resisting hydrodynamic stress (Wildish and Kristmanson, 1997). However, our comprehension is limited by conditions such as water depth hydrodynamic energy and bottom type, rendering it challenging to pinpoint an exact basis for the abundance of this particular trait category. Another important aspect of these communities is their high sensitivity to disturbance, which can indicate the presence of susceptible species. The communities from site 4 primary contributors of dissimilarities were the categories 'tolerant', 'sexual benthic', 'carnivore', 'scavenger', 'under 1 year', 'tubiculous', and 'temporary attachment' organisms. This site, characterised by low hydrodynamic energy and shallow depths, established sandy sediment substrates which are conduits for surface-crawling and carnivore or scavenger taxa (Liu et al., 2019). These communities have short lifespans, small sizes, and tolerance to disturbances with predatory behaviour which may indicate disturbed areas or unpredictable communities (Nunes de Souza et al., 2021; Pandey et al., 2022; Piló et al., 2016). This combination of trait categories establishes communities with opportunistic taxa and high turnover rates. In these two shallow sites, the impact of different levels of hydrodynamic energy seems to shape the bottom type revealing great variability in the categories and trait distribution of the functional structure of the communities. Overall, the BTA uncovered variations of traits and category distribution at the different sites, which can be attributed to the habitat heterogeneity of this region.

4.4. Spatial variation of functional traits and their influence on ecosystem processes

Across the different locations, the relationships between the benthic macrofaunal, their functional traits, and their surrounding environment exhibited varying patterns. These findings suggest that the functioning of ecosystems could differ across habitats, depending on the specific trait composition of the benthic organisms involved. The Feeding method trait is crucial for several ecological processes that provide insights into the sedimentary habitat quality, hydrodynamic conditions, and trophic relationships (Rosenberg, 2001; Bremner et al., 2006; Nunes de Souza et al., 2021). In this study, different patterns emerge for communities between habitats (Fig. 6A). In high dynamic habitats (S2 and S3), a levelled combination of 'suspension feed' and 'deposit feed' organisms were uncovered. Conversely, in the low dynamic habitat at depth (S1), 'suspension feed' organisms dominated, while in the shallow low dynamic habitat (S4), it was the 'deposit feed' and 'predator' organisms. This may indicate that site 1 consumes more pelagic primary producers, consumers, POC and microbes facilitating the transport of carbon from pelagos to benthos (Bremner et al., 2006a,b; Bremner et al., 2006b; Norkko et al., 2013) while site 4 consumes more POC, detritus and microbes, contributing to sediment disruptive activities that enhance decomposition processes (Bremner et al., 2006a,b). The traits Habit and Mobility are able to impact the likelihood of survival, foraging strategies, and potential for particle rework (Nunes de Souza et al., 2021; Pandey et al., 2022). They also contribute to the cycling of energy and elemental components, the development of non-living production, the disruption of food and resources, and the ability to recolonise (Bremner et al., 2006a,b). In these communities, site 1 was the habitat with the most distinct pattern, with a dominance of 'sessile' and 'attached' organisms (Fig. 6B–D). These organisms are dependent on the food resources available in the water column which suggests that in this area they have a high volume of pelagic primary producers, POC, and microbes available for consumption. This ensures the transport of elements from pelagos to the benthos (Bremner et al., 2006, 2006b). The other sites asserted a majority of 'free-living' and 'crawl' organisms but with different backup traits. The categories 'burrow dwelling' and 'tubiculous' were associated with the shallower sites (S3 and S4), which means that they can benefit from the facilitation of the movement of elements from the sediment to water. 'Burrow-dwelling' organisms transport carbon forms within deep surface layers by sediment re-work, indicating that the shallow sites have higher sedimentary habitat quality (Bremner et al., 2006a,b; Nunes de Souza et al., 2021). The traits Lifespan and Body size are responsible for the amount of energy and materials fixed, respired, and transported in the ecosystem, serving as proxies for environmental conditions (Bremner et al., 2006a,b). These are often related to the temporal requirements for the development and growth of individuals and communities (Fig. 6C–7C). They are also considered key predictors of ecosystem functioning as they are extremely affected by habitat loss and disturbance regimes (Norkko et al., 2013). Here, we found a relationship between long-lived species and the deeper sites (S1 and S2) as well as short-lived species with the shallow sites (S3 and S4) as suggested by Alves et al. (2024b). This could indicate environmentally stable conditions at the deeper sites that allow species to develop (Lv et al., 2018). The bigger-sized organisms appear associated with sites 1 and 2, indicating once again stable conditions, conducive to the growth of the community at the deeper sites (Lv et al., 2018). The shallow sites, especially site 4, appeared associated with small-sized and short-lived organisms, which suggests a lack of stability in the conditions and the growth of opportunistic behaviours (Nunes de Souza et al., 2021; Piló et al., 2016). The Larval development and Egg development traits serve to better evaluate the recovery processes, recruitment, and dispersal potential of the communities (Beauchard et al., 2017). We have found that sites 1, 2 and 3 harboured predominantly 'pelagic planktotrophic' organisms, while site 4 revealed a prevalence for 'benthic direct' organisms (Fig. 7A). On the other hand, 'sexual pelagic' organisms appeared associated with deeper sites (S1 and S2) and 'sexual brooded' organisms appeared associated with shallow sites (S3 and S4) (Fig. 7B). This suggests that the deeper sites have greater dispersal strategies, while shallower sites have a lower capacity for dispersal or recruitment (Paganelli et al., 2012; Liu et al., 2019). This allows to

understand the community's elasticity and their ability to maintain or recover after disturbances (Bremner et al., 2006a,b). The Sensitivity to disturbance trait assesses the ecological status of the benthic macrofaunal communities, providing insight into the resilience capacity and vulnerability state (Fig. 7D) (Carvalho et al., 2006; Piló et al., 2016). Our results, indicate that sites 1, 2 and 3 are mostly associated with 'sensitive to disturbance'. In contrast, site 4 exhibits a more even distribution of 'sensitive to disturbance', 'indifferent to disturbance' and 'tolerant to disturbance'. This might be explained by the sedimentary conditions of site 4 as the index AMBI is significantly dependent on the substrate type, grain size, and organic matter content (Borja et al., 2000; Piló et al., 2016; Wetzel et al., 2012). Also, this trait may be less influenced by currents, water mass properties, or depth than sediment composition, leading to a frail variation pattern. Of the eight biological traits analysed, most displayed clear variation patterns, indicating the presence of distinct dynamic macrofaunal communities that correspond to distinct environmental conditions (Fig. 5).

5. Conclusion

This study reveals complex relationships between benthic macrofaunal communities along the Northwest Iberian coast and their environmental conditions. It highlights the influence of site-specific conditions on ecosystem functions, functional measures and trait composition. Although the analyses revealed no significant differences in the factor depth, it remains an important structuring agent for benthic communities, as it plays a crucial role in influencing other important structuring factors. Some of these factors are sediment composition, light availability, hydrodynamics, and bottom type which in turn seem to shape the functional structure of the communities. The sites in highly dynamic (rocky bottoms) habitats exhibit a fulfilled functional niche space, rendering them more resilient to such changes and less prone to loss of function. The sites in low dynamic habitats exhibit fewer species occupying the available functional niche space and therefore exhibit a frail functionality and heightened vulnerability to alterations in their environment. Within these, Biological Trait Analysis (BTA) identified key traits contributing to community dissimilarities, with distinct patterns emerging between deep and shallow sites, further emphasising the influence of habitat heterogeneity on ecosystem processes. These communities exhibit different functional structures, delivering different functions into the ecosystem. To our knowledge, this study represents the first application of BTA in this region, which allows to establish a direct connection between the environmental processes and the ecological functioning of the ecosystem. These efforts also contribute to the baseline data in terms of both species and functional diversity of the benthic macrofaunal communities within this region. Future studies should further explore these approaches to enhance our predictive capabilities and ensure the functioning of ecosystems.

CRediT authorship contribution statement

Catarina M. Alves: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Marisa A. Gomes:** Writing – review & editing, Methodology. **Jesus S. Troncoso:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Pedro T. Gomes:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

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.

Acknowledgements

C.M.A. (PD/BD/150365/2019) and M.A.G. (PD/BD/143088/2018) were supported by a PhD Fellowship from the PhD program on Science, Technology and Marine Management (Do*Mar) co-financed by FCT and FSE through the Norte Portugal Regional Operational Programme (NORTE 2020). This study was co-supported by the project ATLANTIDA (ref. NORTE-01-0145-FEDER-000040), supported by the Norte Portugal Regional Operational Programme (NORTE 2020), under the PORTUGAL 2020 Partnership Agreement and through the European Regional Development Fund (ERDF). This work was also supported by the "Contrato-Programa" UIDB/04050/2020 (https://doi.org/10.54499/UIDB/04050/2020) funded by national funds through the FCT I.P. and through LA/P/0069/2020 (https://doi.org/10.54499/LA/P/0069/2020) granted to the Associate Laboratory ARNET.

Annex A.

Table A1
Fixed effects for the generalized linear mixed model (GLMM) for functional richness (FRic), functional dispersion (FDis), functional divergence (FDiv), functional evenness (FEve) Rao's quadratic entropy (RaoQ), and functional redundancy (FRed).

	Estimate	Std.Error	t value	Pr (>|z|)
Functional Richness				
Intercept	3.45 e^{-04}	4.67 e^{-05}	7.402	1.35 e^{-13} ***
Depth D26	1.13 e^{-04}	6.92 e^{-05}	1.634	0,1023
Bottom SAN	1.37 e^{-04}	6.65 e^{-05}	2.070	**0.0384** *
Functional Divergence				
Intercept	1.4724	0.03587	41,041	<2 e^{-16} ***
Depth D26	−0.1596	0,04217	−3.787	**0,00015** ***
Bottom SAN	−0,2248	0,04171	−5.391	**7** e^{-8} ***
Functional Dispersion				
Intercept	0.1493	0,0135	10,999	<2 e^{-16} ***
Depth D26	−0.0041	0,0155	−0.264	0,792
Bottom SAN	0.0094	0,0155	0.0608	0.543

(*continued on next page*)

Table A1 (*continued*)

	Estimate	Std.Error	t value	Pr (>|z|)
Functional Evenness				
Intercept	1.8597	0,1134	16.394	$<2\ e^{-16}$ ***
Depth D26	0.0072	0,1307	0,056	0,956
Bottom SAN	−0,0781	0,1305	−0.598	0.550
RaoQ				
Intercept	0,02098	0,00298	7.044	$1.86\ e^{-12}$ ***
Depth D26	−0,00125	0,00339	−0.371	0,711
Bottom SAN	0,00113	0,00339	0.332	0.740
Functional Redundancy				
Intercept	2.0348	0.1360	14.965	$<2\ e^{-16}$ ***
Depth D26	0.3444	0.1535	2.243	**0,0249** *
Bottom SAN	0.1544	01541	1.002	0.3162

Note.
*Significant at 0.05 level.
**Significant at 0.001 level.
***Significant at < 0.001 level.

Table A2
– List of sampling taxa after 3 months of colonisation across four different sites (S1 – site 1, S2 – site 2, S3 -site 3, S4 – site 4).

Sampled Species			
Arthropoda	*Pachygrapsus marmoratus*	*Spiralinella spiralis*	*Eumida sanguinea*
Gammaropsis maculata	*Eurynome spinosa*	*Crepidula fornicata*	*Syllis vittata*
Photis longicaudata	*Liocarcinus navigator*	*Tectura virginea*	*Syllis gracilis*
Aora gracilis	*Nebalia* sp.	*Cyrillia linearis*	*Syllis prolifera*
Lembos websteri	*Janira maculosa*	*Trivia arctica*	*Syllis armillaris*
Microdeutopus chelifer	*Uromunna* sp.	*Aplysia punctata*	*Syllis krohnii*
Monocorophium sextonae	*Anthura gracilis*	*Limacia clavigera*	*Eurysyllis tuberculata*
Monocorophium acherusicum	*Astacilla damnoniensis*	*Felimare villafranca*	*Myrianida prolifera*
Elasmopus rapax	*Cleantis prismatica*	*Ancula gibbosa*	*Odontosyllis gibba*
Abludomelita gladiosa	*Paragnathia formica*	*Doto coronata*	*Glycera tridactyla*
Gammarella fucicola	*Limnoria* sp.	*Mytilus galloprovincialis*	*Paleanotus bellis*
Ericthonius brasiliensis	*Idotea pelagica*	*Musculus costulatus*	*Psamathe fusca*
Jassa falcata	*Stenosoma lancifer*	*Musculus discors*	*Capitella capitata*
Stenothoe tergestina	*Dynamene bidentata*	*Hiatella arctica*	*Notomastus latericeus*
Phtisica marina	*Cymodoce truncata*	*Heteronomia squamula*	*Golfingia* sp.
Caprella acanthifera	*Zeuxo holdichi*	*Anomia ephippium*	**Echinodermata**
Caprella liparotensis	*Apseudes talpa*	*Mimachlamys varia*	*Paracentrotus lividus*
Apherusa bispinosa	*Diastylis rugosa*	*Venerupsis corrugata*	*Asterina gibbosa*
Apherusa jurinei	*Perforatus perforatus*	*Abra alba*	*Amphipholis squamata*
Iphimedia minuta	*Achelia echinata*	*Boreochiton ruber*	*Ophiothrix fragilis*
Apolochus neapolitanus	*Ammothella longipes*	*Acanthochitona crinita*	*Antedon bifida*
Dexamine spinosa	*Ammothella longioculata*	**Annelida**	*Ocnus lacteus*
Lepidepecreum longicorne	*Nymphon gracile*	*Platynereis dumerilii*	*Pawsonia saxicola*
Microprotopus longimanus	**Mollusca**	*Hediste diversocolor*	**Platyhelminthes**
Microprotopus maculatus	*Steromphala umbilicalis*	*Harmothoe impar*	*Leptoplana tremellaris*
Ampelisca spinipes	*Steromphala pennanti*	*Harmothoe glabra*	*Stylochoplana maculata*
Nototropis swammerdamei	*Jujubinus exasperatus*	*Lepidonotus clava*	*Stylostomum ellipse*
Nototropis guttatus	*Jujubinus striatus*	*Lepidonotus squamatus*	*Comoplana agilis*
Gammarus locusta	*Tricolia pullus*	*Pholoe minuta*	*Prosthiostomum siphunculus*
Pereionotus testudo	*Rissoa parva*	*Sthenelais boa*	*Cycloporus papillosus*
Eualus cranchii	*Crisilla semistriata*	*Eupolymnia nebulosa*	**Cnidaria**
Eualus occultus	*Alvania* sp.	*Nicolea venustula*	*Actinia equina*
Hippolyte varians	*Retusa truncatula*	*Branchiomma bombyx*	*Corynactis viridis*
Athanas nitescens	*Melanella alba*	*Pseudopotamilla reniformis*	*Haliclystus auricula*
Pilumnus hirtellus	*Vitreolina philippi*	*Aphelochaeta marioni*	**Nemertea**
Macropodia rostrata	*Curveulima dautzenbergi*	*Cirratulus cirratus*	*Oerstedia dorsalis*
Macropodia linaresi	*Tritia incrassata*	*Spirobranchus triqueter*	**Chordata**
Macropodia tenuirostris	*Ocinebrina aciculata*	*Spirobranchus lamarki*	*Diplecogaster bimaculata*
Pisidia longicornis	*Bittium reticulatum*	*Malacoceros fuliginosus*	*Corella eumyota*
Pagurus bernhardus	*Odostomia turrita*	*Malacoceros vulgaris*	*Nerophis lumbriciformis*

References

Airoldi, L., Cinelli, F., 1997. Effects of sedimentation on subtidal macroalgal assemblages: an experimental study from a mediterranean rocky shore. J. Exp. Mar. Biol. Ecol. 215 (2), 269–288. https://doi.org/10.1016/S0022-0981(96)02770-0.

Alsterberg, C., Roger, F., Sundbäck, K., Juhanson, J., Hulth, S., Hallin, S., Gamfeldt, L., 2017. Habitat Diversity and Ecosystem Multifunctionality — the Importance of Direct and Indirect Effects, pp. 1–10.

Alves, C.M., 2017. Macroalgas formadoras de habitat: Espaço neutro para macrofauna marinha? University of Minho.

Alves, C.M., Gomes, M.A., Neto, R., Troncoso, J., Gomes, P.T., 2024a. Patterns of diversity in subtidal marine macrofaunal communities: insights from a semi-enclosed bay system in the Northeast Atlantic. Regional Studies in Marine Science 72, 103441. https://doi.org/10.1016/j.rsma.2024.103441.

Alves, C.M., Gomes, M.A., Troncoso, J.S., Gomes, P.T., 2024b. Structural and functional diversity patterns of macrofaunal communities from a semi-enclosed inlet of

Northeast Atlantic: the influence of environmental conditions. Estuar. Coast Shelf Sci. 296, 108575 https://doi.org/10.1016/j.ecss.2023.108575.
Anderson, M.J., 2017. Permutational Multivariate Analysis of Variance (PERMANOVA). Wiley StatsRef: Statistics Reference Online, pp. 1–15. https://doi.org/10.1002/9781118445112.stat07841.
Bakun, A., Black, B.A., Bograd, S., Cruz, S., 2015. Anticipated effects of climate change on coastal upwelling ecosystems. June. https://doi.org/10.1007/s40641-015-0008-4.
Bartomeus, I., 2015. fundiv: analyzing functional trait diversity. https://github.com/ibartomeus/fundiv.
Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Software 67 (1), 1–48. https://doi.org/10.18637/jss.v067.i01.
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. Indicat. 76, 81–96. https://doi.org/10.1016/j.ecolind.2017.01.011.
Bertness, M.D., Gaines, S.D., Stephens, E.G., Yund, P.O., 1992. Components of recruitment in populations of the acorn barnacle Semibalanus balanoides (Linnaeus). J. Exp. Mar. Biol. Ecol. 156 (2), 199–215. https://doi.org/10.1016/0022-0981(92)90246-7.
Blockley, D.J., Chapman, M.G., 2006. Recruitment determines differences between assemblages on shaded or unshaded seawalls. Mar. Ecol. Prog. Ser. 327 (December 2006), 27–36. https://doi.org/10.3354/meps327027.
Boaventura, D., Ré, P., Da Fonseca, L.C., Hawkins, S.J., 2002. Intertidal rocky shore communities of the continental Portuguese coast: analysis of distribution patterns. Mar. Ecol. 23 (1), 69–90. https://doi.org/10.1046/j.1439-0485.2002.02758.x.
Borja, A., Franco, J., Pérez, V., 2000. A marine Biotic Index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. Mar. Pollut. Bull. 40 (12), 1100–1114. https://doi.org/10.1016/S0025-326X(00)00061-8.
Breine, N.T., 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 (April), 173–184. https://doi.org/10.1016/j.ecss.2018.09.012.
Bremner, J., Paramor, O.A.L., Frid, C.L.J., 2006a. Developing a methodology for incorporating ecological structure and functioning into designation of Special Areas of Conservation (SAC) in the 0-12 nautical mile zone. In: School of Biological Sciences. University of Liverpool. http://www.mrag.co.uk/Documents/gb0921/EN_SAC_final_report.pdf.
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. Indicat. 6 (3), 609–622. https://doi.org/10.1016/j.ecolind.2005.08.026.
Cacabelos, E., Gestoso, L., Troncoso, J., 2008. Macrobenthic fauna in the Ensenada de San Simón (Galicia, north-western Spain). J. Mar. Biol. Assoc. U. K. 88 (2), 237–245. https://doi.org/10.1017/S0025315408000660.
Cadotte, M.W., Carscadden, K., Mirotchnick, N., 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. J. Appl. Ecol. 48 (5), 1079–1087. https://doi.org/10.1111/j.1365-2664.2011.02048.x.
Cardoso, P., Mammola, S., Rigal, F., Carvalho, J., 2022. Biodiversity assessment tools. Package 'BAT. https://doi.org/10.1111/2041-210X.12310.
Carreira-Flores, D., Neto, R., Ferreira, H., Cabecinha, E., Díaz-Agras, G., Gomes, P.T., 2020. Artificial substrates as sampling devices for marine epibenthic fauna: a quest for standardization. Regional Studies in Marine Science 37, 101331. https://doi.org/10.1016/j.rsma.2020.101331.
Carvalho, S., Gaspar, M.B., Moura, A., Vale, C., Antunes, P., Gil, O., da Fonseca, L.C., Falcão, M., 2006. The use of the marine biotic index AMBI in the assessment of the ecological status of the Óbidos lagoon (Portugal). Mar. Pollut. Bull. 52 (11), 1414–1424. https://doi.org/10.1016/j.marpolbul.2006.04.004.
Champely, S., Chessel, D., 2002. Measuring biological diversity using Euclidean metrics. Environ. Ecol. Stat. 9 (2), 167–177. https://doi.org/10.1023/A:1015170104476.
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), 1–12. https://doi.org/10.1038/s41597-022-01442-y.
Coleman, N., Cuff, W., Moverley, J., Gason, A.S.H., Heislers, S., 2007. Depth, sediment type, biogeography and high species richness in shallow-water benthos. Mar. Freshw. Res. 58 (3), 293–305. https://doi.org/10.1071/MF06098.
Delfan, N., Shojaei, M.G., Naderloo, R., 2021. Patterns of structural and functional diversity of macrofaunal communities in a subtropical mangrove ecosystem. Estuar. Coast Shelf Sci. 252, 107288 https://doi.org/10.1016/j.ecss.2021.107288.
Denny, M.W., 2006. Ocean waves, nearshore ecology, and natural selection. Aquat. Ecol. 40 (4), 439–461. https://doi.org/10.1007/s10452-004-5409-8.
Dias, J.M.A., Gonzalez, R., Garcia, C., Diaz-del-Rio, V., 2002a. Sediment distribution patterns on the Galicia-Minho continental shelf. Prog. Oceanogr. 52 (2–4), 215–231. https://doi.org/10.1016/S0079-6611(02)00007-1.
Dias, J.M.A., Jouanneau, J.M., Gonzalez, R., Araújo, M.F., Drago, T., Garcia, C., Oliveira, A., Rodrigues, A., Vitorino, J., Weber, O., 2002b. Present day sedimentary processes on the northern Iberian shelf. Prog. Oceanogr. 52 (2–4), 249–259. https://doi.org/10.1016/S0079-6611(02)00009-5.
Díaz, S., Cabido, M., 2001. Vive la différence: plant functional diversity matters to ecosystem processes. Ecol. Evol. 16, 646–655. https://doi.org/10.1348/026151005X50753.
Dissanayake, N.G., Frid, C.L.J., Drylie, T.P., Caswell, B.A., 2018. Ecological functioning of mudflats: global analysis reveals both regional differences and widespread conservation of functioning. Mar. Ecol. Prog. Ser. 604, 1–20. https://doi.org/10.3354/meps12728.
Dolbeth, M., Cardoso, P.G., Grilo, T.F., Bordalo, M.D., Raffaelli, D., Pardal, M.A., 2011. Long-term changes in the production by estuarine macrobenthos affected by multiple stressors. Estuar. Coast Shelf Sci. 92 (1), 10–18. https://doi.org/10.1016/j.ecss.2010.12.006.
Encyclopedia of Life, 2023. http://eol.org.
Falkenberg, L.J., Scanes, E., Ducker, J., Ross, P.M., 2021. Biotic habitats as refugia under ocean acidification. Conservation Physiology 9, 1–16. https://doi.org/10.1093/conphys/coab077.
Frid, C.L.J., Paramor, O.A.L., Brockington, S., Bremner, J., 2008. Incorporating ecological functioning into the designation and management of marine protected areas. Hydrobiologia 606 (1), 69–79. https://doi.org/10.1007/s10750-008-9343-y.
Gamito, S., Furtado, R., 2009. Feeding diversity in macroinvertebrate communities: a contribution to estimate the ecological status in shallow waters. Ecol. Indicat. 9 (5), 1009–1019. https://doi.org/10.1016/j.ecolind.2008.11.012.
Gaudêncio, M.J., Cabral, H.N., 2007. Trophic structure of macrobenthos in the Tagus estuary and adjacent coastal shelf. Hydrobiologia 587 (1), 241–251. https://doi.org/10.1007/s10750-007-0686-6.
Glasby, T.M., 1999. Interactive effects of shading and proximity to the seafloor on the development of subtidal epibiotic assemblages. Mar. Ecol. Prog. Ser. 190 (December 1999), 113–124. https://doi.org/10.3354/meps190113.
Gomes, M.A., Alves, C.M., Faria, F., Troncoso, J.S., Gomes, P.T., 2024. Untangling coastal diversity: how habitat complexity shapes demersal and benthopelagic assemblages in NW iberia. J. Mar. Sci. Eng. 12 (4) https://doi.org/10.3390/jmse12040538.
Gomez-Gesteira, M., Beiras, R., Presa, P., Vilas, F., 2011. Coastal processes in northwestern Iberia , Spain. Continent. Shelf Res. 31 (5), 367–375. https://doi.org/10.1016/j.csr.2011.01.002.
Griffin, J.N., O'Gorman, E.J., Emmerson, M.C., Jenkins, S.R., Klein, A.-M., Michel, Loreau, Symstad, A., 2009. Biodiversity and the stability of ecosystem functioning. Etica e Politica 15 (1), 583–605. https://doi.org/10.1093/acprof.
Gusmao, J.B., Brauko, K.M., Eriksson, B.K., Lana, P.C., 2016. Functional diversity of macrobenthic assemblages decreases in response to sewage discharges. Ecol. Indicat. 66, 65–75. https://doi.org/10.1016/j.ecolind.2016.01.003.
Hajializadeh, P., Safaie, M., Naderloo, R., Shojaei, M.G., Gammal, J., Villnäs, A., Norkko, A., 2020. Species composition and functional traits of macrofauna in different mangrove habitats in the Persian gulf. Front. Mar. Sci. 7 https://doi.org/10.3389/fmars.2020.575480.
Han, C., Xu, Z., Liu, X., 2021. Characteristics of macrofaunal assemblages and their relationships with environmental factors in a semi-enclosed bay. Mar. Pollut. Bull. 167 https://doi.org/10.1016/j.marpolbul.2021.112348.
Harrell Jr, F.E., Dupont, C., 2023. Harrell Miscellaneous. R Package "Hmisc 1–487, Version 5.1-0. https://hbiostat.org/R/Hmisc/.
Hayward, P.J., Ryland, J.S. (Eds.), 1995. Handbook Marine Fauna of North-West Europe. Oxford Univresity Press.
Henseler, C., Nordström, M.C., Törnroos, A., Snickars, M., Pecuchet, L., Lindegren, M., Bonsdorff, E., 2019. Coastal habitats and their importance for the diversity of benthic communities: a species- and trait-based approach. Estuar. Coast Shelf Sci. 226 https://doi.org/10.1016/j.ecss.2019.106272.
Hessler, R.R., 1981. Evolution of Arthropod Locomotion: A Crustacean Model. In: Herreid, C.F., Fourtner, C.R. (Eds.), Locomotion and Energetics in Arthropods. Springer. https://books.google.com/books?id=9ej4BwAAQBAJ&pg=PA9.
Hewitt, J.E., Thrush, S.F., Dayton, P.D., 2008. Habitat variation, species diversity and ecological functioning in a marine system. J. Exp. Mar. Biol. Ecol. 366 (1–2), 116–122. https://doi.org/10.1016/j.jembe.2008.07.016.
Hily, C., Bouteille, M., 1999. Modifications of the specific diversity and feeding guilds in an intertidal sediment colonized by an eelgrass meadow (Zoestera marina) (Brittany, France). C.R.Acad.Sci. Paris, Science de La Vie 322, 1121–1131.
Hurd, C.L., 2000. Water Motion, Marine Macroalgal Physiology, and Production, vol. 472. Phycological Society of America, pp. 453–472.
Hurd, C.L., 2015. Slow-flow habitat as refugia for coastal calcifiers from ocean. Phycological Society of America 605, 599–605. https://doi.org/10.1111/jpy.12307.
Hurlbert, S.H., 1971. The nonconcept of species diversity : a critique and alternative parameters. Ecological Society of America 52 (4), 577–586.
Jumars, P.A., Dorgan, K.M., Lindsay, S.M., 2015. Diet of worms emended: an update of polychaete feeding guilds. Ann. Rev. Mar. Sci 7, 497–520. https://doi.org/10.1146/annurev-marine-010814-020007.
Konar, B., Iken, K., Edwards, M., 2009. Depth-stratified community zonation patterns on Gulf of Alaska rocky shores. Mar. Ecol. 30 (1), 63–73. https://doi.org/10.1111/j.1439-0485.2008.00259.x.
Kraufvelin, P., Perus, J., Bonsdorff, E., 2011. Scale-dependent distribution of soft-bottom infauna and possible structuring forces in low diversity systems. Mar. Ecol. Prog. Ser. 426, 13–28. https://doi.org/10.3354/meps09038.
Laliberte, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91 (1), 299–305. https://doi.org/10.1890/08-2244.1.
Laliberté, E., Legendre, P., Shipley, B., 2014. Measuring Functional Diversity (FD) from Multiple Traits, and Other Tools for Functional Ecology 1 (0–12.1).
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. Indicat. 115 https://doi.org/10.1016/j.ecolind.2020.106379.
Lam-Gordillo, O., Baring, R., Dittmann, S., 2021. Taxonomic and functional patterns of benthic communities in southern temperate tidal flats. Front. Mar. Sci. 8, 1–19. https://doi.org/10.3389/fmars.2021.723749.
Lincoln, R.J., 1979. British marine Amphipoda: gammaridea. In: British Museum (Natural History). British Museum (Natural History).
Liu, K., Lin, H., He, X., Huang, Y., Li, Z., Lin, J., Mou, J., Zhang, S., Lin, L., Wang, J., Sun, J., 2019. Functional trait composition and diversity patterns of marine

macrobenthos across the Arctic Bering Sea. Ecol. Indicat. 102, 673–685. https://doi.org/10.1016/j.ecolind.2019.03.029.
Llanos, E.N., Saracho Bottero, M.A., Jaubet, M.L., Elías, R., Garaffo, G.V., 2020. Functional diversity in the intertidal macrobenthic community at sewage-affected shores from Southwestern Atlantic. Mar. Pollut. Bull. 157, 111365 https://doi.org/10.1016/j.marpolbul.2020.111365.
Lotze, H.K., 2021. Ll Marine biodiversity conservation ll. Curr. Biol. 31 (19), R1190–R1195. https://doi.org/10.1016/j.cub.2021.06.084.
Lourido, A., Cacabelos, E., Troncoso, J.S., 2008a. Patterns of distribution of the polychaete fauna in subtidal soft sediments of the Ría de Aldán (north-western Spain). J. Mar. Biol. Assoc. U. K. 88 (2), 263–275. https://doi.org/10.1017/S0025315408000696.
Lourido, A., Moreira, J., Troncoso, J.S., 2008b. Assemblages of peracarid crustaceans in subtidal sediments from the Ría de Aldán (Galicia, NW Spain). Helgol. Mar. Res. 62 (4), 289–301. https://doi.org/10.1007/s10152-008-0116-9.
Lourido, A., Moreira, J., Troncoso, J.S., 2010. Distribución espacial de la macrofauna bentónica de sedimentos submareales de la ría de aldán (galicia, noroeste de españa). Sci. Mar. 74 (4), 705–715. https://doi.org/10.3989/scimar.2010.74n4705.
Lv, W., Zhou, W., Zhao, Y., 2018. Macrobenthos functional groups as indicators of ecological restoration in reclaimed intertidal wetlands of China's Yangtze Estuary. Regional Studies in Marine Science 22, 93–100. https://doi.org/10.1016/j.rsma.2018.06.003.
Marine Life Information Network (MarLIN), 2023. The marine biological association of the UK. https://www.marlin.ac.uk/.
Martins, V., Dubert, J., Jouanneau, J.M., Weber, O., da Silva, E.F., Patinha, C., Alveirinho Dias, J.M., Rocha, F., 2007. A multiproxy approach of the Holocene evolution of shelf-slope circulation on the NW Iberian Continental Shelf. Mar. Geol. 239 (1–2), 1–18. https://doi.org/10.1016/j.margeo.2006.11.001.
Mason, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111 (1), 112–118. https://doi.org/10.1111/j.0030-1299.2005.13886.x.
McClain, C.R., Chao, S.-Y., Atkinson, L.P., Blanton, J.O., De Castillejo, F., 1986. Wind-driven upwelling in the vicinity of cape finisterre, Spain. J. Geophys. Res. 91 (C7), 8470. https://doi.org/10.1029/jc091ic07p08470.
McQuaid, C.D., Lindsay, T.L., 2007. Wave exposure effects on population structure and recruitment in the mussel perna perna suggest regulation primarily through availability of recruits and food, not space. Mar. Biol. (Berl.) 151 (6), 2123–2131. https://doi.org/10.1007/s00227-007-0645-9.
Momota, K., 2021. Potential impacts of marine urbanization on benthic macrofaunal diversity. Sci. Rep. 1–12 https://doi.org/10.1038/s41598-021-83597-z.
Montes, A., Vázquez, E., Peteiro, L.G., Olabarria, C., 2021. Dynamics and processes influencing recruitment of the invasive mussel xenostrobus securis and the coexisting indigenous mytilus galloprovincialis in North-Western Spain. Aquat. Invasions 16 (3), 391–414. https://doi.org/10.3391/ai.2021.16.3.02.
Mouchet, M.A., Villéger, S., Mason, N.W.H., Mouillot, D., 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Funct. Ecol. 24 (4), 867–876. https://doi.org/10.1111/j.1365-2435.2010.01695.x.
Navarro-Barranco, C., Tierno-de-Figueroa, J.M., Guerra-García, J.M., Sánchez-Tocino, L., García-Gómez, J.C., 2013. Feeding habits of amphipods (Crustacea: malacostraca) from shallow soft bottom communities: comparison between marine caves and open habitats. J. Sea Res. 78, 1–7. https://doi.org/10.1016/j.seares.2012.12.011.
Naylor, E.E., 1972. British Marine Isopods. Academic Press Inc.
Noisette, F., Pansch, C., Wall, M., Wahl, M., Hurd, C.L., 2022. Role of hydrodynamics in shaping chemical habitats and modulating the responses of coastal benthic systems to ocean global change. Global Change Biol. 28 (12), 3812–3829. https://doi.org/10.1111/gcb.16165.
Norkko, A., Villnas, A., Norkko, J., Valanko, S., Pilditch, C., 2013. Size matters: implications of the loss of large individuals for ecosystem function. Sci. Rep. 3 (2646) https://doi.org/10.1038/srep02646.
Nowell, A.R.M., Jumars, P.A., 1984. Flow environments of aquatic benthos. Annu. Rev. Ecol. Systemat. 15, 303–328.
Nunes de Souza, J.V., Martins Vieira, M.L., De Assis, J.E., Zanardi - Lamardo, E., Gomes, P.B., Botelho de Souza, J.R., 2021. Responses of functional traits of macrobenthic communities on the presence of Polycyclic Aromatic Hydrocarbons contamination in three tropical estuaries. Estuar. Coast Shelf Sci. 250 https://doi.org/10.1016/j.ecss.2020.107105.
Nunes, M., Coelho, J.P., Cardoso, P.G., Pereira, M.E., Duarte, A.C., Pardal, M.A., 2008. The macrobenthic community along a mercury contamination in a temperate estuarine system (Ria de Aveiro, Portugal). Sci. Total Environ. 5 (3) https://doi.org/10.1016/j.scitotenv.2008.07.009, 0–8.
Paganelli, D., Marchini, A., Occhipinti-Ambrogi, A., 2012. Functional structure of marine benthic assemblages using biological traits analysis (BTA): a study along the emilia-romagna coastline (Italy, north-west adriatic sea). Estuar. Coast Shelf Sci. 96 (1), 245–256. https://doi.org/10.1016/j.ecss.2011.11.014.
Palomares, M.L.D., Pauly, D., 2023. SeaLifeBase. www.sealifebase.org.
Pandey, V., Jha, D.K., Kumar, P.S., Santhanakumar, J., Venkatnarayanan, S., Prince Prakash Jebakumar, J., Dharani, G., 2022. Effect of multiple stressors on the functional traits of sub-tidal macrobenthic fauna: a case study of the southeast coast of India. Mar. Pollut. Bull. 175 https://doi.org/10.1016/j.marpolbul.2022.113355.
Pardo, J.B., Nobre, D., Monteiro, J.N., Sousa, P.M., Costa, E.F.S., Baptista, V., Ovelheiro, A., Vieira, V.M.N.C.S., Chícharo, L., Gaspar, M., Erzini, K., Kay, S., Queiroga, H., Teodósio, M.A., Leitão, F., 2021. Climate change vulnerability assessment of the main marine commercial fish and invertebrates of Portugal. Sci. Rep. 1–18. https://doi.org/10.1038/s41598-021-82595-5.
Patrício, J., Adão, H., Neto, J.M., Alves, A.S., Traunspurger, W., Marques, J.C., 2012. Do nematode and macrofauna assemblages provide similar ecological assessment information? Ecol. Indicat. 14, 124–137. https://doi.org/10.1016/j.ecolind.2011.06.027.
Paz-Ríos, C.E., Pech, D., Mariño-Tapia, I., Simões, N., 2020. Influence of bottom environment conditions and hydrographic variability on spatiotemporal trends of macrofaunal amphipods on the Yucatan continental shelf. Continent. Shelf Res. 198 https://doi.org/10.1016/j.csr.2020.104098.
Pearson, T.H., Rosenberg, R., 1987. Feast and famine: structuring factors in marine benthic communities. In: Giller, J.H.R., Gee, P. (Eds.), The 27th Symposium of the British Ecological Society, Aberystwyth 1986, The 27th Symposium of the British Ecological Society, Aberystwyth 1986. Blackwell Scientific Publications, pp. 373–395, 373-395. Blackwell scientific publications, oxford.
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.
Petchey, O.L., Hector, A., Gaston, K.J., 2004. How do different measures of functional diversity perform? Ecology 85 (3), 847–857. https://doi.org/10.1890/03-0226.
Pielou, E.C., 1966. The measurement of diversity in different types of biological collections. J. Theor. Biol. 13, 131–144. https://doi.org/10.1016/0022-5193(66)90013-0.
Piló, D., Ben-Hamadou, R., Pereira, F., Carriço, A., Pereira, P., Corzo, A., Gaspar, M.B., Carvalho, S., 2016. How functional traits of estuarine macrobenthic assemblages respond to metal contamination? Ecol. Indicat. 71, 645–659. https://doi.org/10.1016/j.ecolind.2016.07.019.
Piló, D., Pereira, F., Carriço, A., Cúrdia, J., Pereira, P., Gaspar, M.B., Carvalho, S., 2015. Temporal variability of biodiversity patterns and trophic structure of estuarine macrobenthic assemblages along a gradient of metal contamination. Estuar. Coast Shelf Sci. 1–14. https://doi.org/10.1016/j.ecss.2015.06.018.
Pinto, R., Patrício, J., Baeta, A., Fath, B.D., Neto, J.M., Marques, J.C., 2009. Review and evaluation of estuarine biotic indices to assess benthic condition. Ecol. Indicat. 1–25. https://doi.org/10.1016/j.ecolind.2008.01.005.
Pirtle, J.L., Ibarra, S.N., Eckert, G.L., 2012. Nearshore subtidal community structure compared between inner coast and outer coast sites in Southeast Alaska. Polar Biol. 35 (12), 1889–1910. https://doi.org/10.1007/s00300-012-1231-2.
Polytraits, 2023. A Database on Biological Traits of Polychaetes. Hellenic Centre for Marine Research. http://polytraits.lifewatchgreece.eu/.
Queirós, A.M., Birchenough, S.N.R., Bremner, J., Godbold, J.A., Parker, R.E., Romero-Ramirez, A., Reiss, H., Solan, M., Somerfield, P.J., Van Colen, C., Van Hoey, G., Widdicombe, S., 2013. A bioturbation classification of European marine infaunal invertebrates. Ecol. Evol. 3 (11), 3958–3985. https://doi.org/10.1002/ece3.769.
Quell, F., Schratzberger, M., Beauchard, O., Bruggeman, J., Webb, T., 2021. Biological trait profiles discriminate between native and non-indigenous marine invertebrates. Aquat. Invasions 16 (4), 571–600. https://doi.org/10.3391/AI.2021.16.4.01.
Rand, K., Logerwell, E., Bluhm, B., Chenelot, H., Danielson, S., Iken, K., Sousa, L., 2018. Using biological traits and environmental variables to characterize two Arctic epibenthic invertebrate communities in and adjacent to Barrow Canyon. Deep-Sea Res. Part II Top. Stud. Oceanogr. 152 (July 2017), 154–169. https://doi.org/10.1016/j.dsr2.2017.07.015.
Rao, R., 1982. Diversity and dissimilarity. Theoritical Population Biology 21 (1), 24–43. https://ac.els-cdn.com/0040580982900041/1-s2.0-0040580982900041-main.pdf?_tid=f24f6d3a-94c8-4de7-b11e-b2c826a3e726&acdnat=1542633469_d6b4b2341bd4b5b7747b44028003340d.
Rasband, W.S., 1997. ImageJ. National Institutes of Health, Bethesda, Maryland, USA. https://imagej.net/ij/.
Ríos, A.F., Pérez, F.F., Fraga, F., 1992. Water masses in the upper and middle North Atlantic ocean east of the azores. Deep-Sea Res., Part A 39 (3–4), 645–658. https://doi.org/10.1016/0198-0149(92)90093-9.
Rosa-Santos, P., Veloso-Gomes, F., Taveira-Pinto, F., Silva, R., Pais-Barbosa, J., 2009. Evolution of coastal works in Portugal and their interference with local morphodynamics. J. Coast Res. 2009 (SPEC. ISSUE 56), 757–761.
Rosenberg, R., 2001. Marine benthic faunal successional stages and related sedimentary activity. Sci. Mar. 65 (Suppl. 2), 107–119. https://doi.org/10.3989/scimar.2001.65s2107.
Rosenberg, Rutger, 1995. Benthic marine fauna structured by hydrodynamic processes and food availability. Neth. J. Sea Res. 34 (4), 303–317. https://doi.org/10.1016/0077-7579(95)90040-3.
Rosón, G., Cabanas, J.M., Pérez, F.F., 2008. Hidrografía y dinámica de la ría de Vigo. Un sistema de afloramiento. La . Una Aproximación Integral Al Ecosistema Marino de La Ría de Vigo 51–84. Una Aproximación Integral Al Ecosistema Marino de La Ría de Vigo. http://hdl.handle.net/10261/115885.
Rubal, M., Maldre, K., Sousa-Pinto, I., Veiga, P., 2021. Current distribution and abundance of Austrominius modestus (Darwin, 1854) and other non-indigenous barnacles along the northern coast of Portugal. Regional Studies in Marine Science 41, 101586. https://doi.org/10.1016/j.rsma.2020.101586.
Ruppert, E.E., Fox, R.S., Barnes, R.D., 2004. In: Invertebrate Zoology: A Functional Evolutionary Approach, , Seventh Editionvii-xvii, 1-936. Thomson, Brooks/Cole, pp. I1–I26.
Saeedi, H., Warren, D., Brandt, A., 2022. The environmental drivers of benthic fauna diversity and community composition. Front. Mar. Sci. 9, 1–16. https://doi.org/10.3389/fmars.2022.804019.
Saldanha, L., 1995. Fauna submarina atlântica. In: Castro, F.L. (Ed.), Publicações Europa-América, Lda.
Shannon, C.E., 1948. A mathematical theory of communication. Bell System Technical Journal 27 (3), 379–423. https://doi.org/10.1002/j.1538-7305.1948.tb01338.x.

Simpson, E.H., 1949. Measurement of diversity. Nature 163, 688. https://doi.org/10.1038/163688a0.
Sivadas, S.K., Singh, D.P., Saraswat, R., 2020. Functional and taxonomic (α and β) diversity patterns of macrobenthic communities along a depth gradient (19–2639 m): a case study from the southern Indian continental margin. Deep-Sea Res. Part I Oceanogr. Res. Pap. 159, 103250 https://doi.org/10.1016/j.dsr.2020.103250.
Smale, D.A., 2008. Continuous benthic community change along a depth gradient in Antarctic shallows: evidence of patchiness but not zonation. Polar Biol. 31 (2), 189–198. https://doi.org/10.1007/s00300-007-0346-3.
Snelgrove, P.V.R., Butman, C.A., 1994. Animal sediment relationships revisited – cause versus effect. Oceanogr. Mar. Biol. 32, 111–177.
Sokołowski, A., Ziółkowska, M., Balazy, P., Kuklиński, P., Plichta, I., 2017. Seasonal and multi-annual patterns of colonisation and growth of sessile benthic fauna on artificial substrates in the brackish low-diversity system of the Baltic Sea. Hydrobiologia 790 (1), 183–200. https://doi.org/10.1007/s10750-016-3043-9.
Sousa, M.C., Ribeiro, A., Des, M., Gomez-Gesteira, M., DeCastro, M., Dias, J.M., 2019. NW Iberian Peninsula coastal upwelling future weakening: competition between wind intensification and surface heating. Sci. Total Environ., 134808 https://doi.org/10.1016/j.scitotenv.2019.134808.
Sun, X., Dong, J., Hu, C., Zhang, Y., Chen, Y., Zhang, X., 2021. Use of macrofaunal assemblage indices and biological trait analysis to assess the ecological impacts of coastal bivalve aquaculture. Ecol. Indicat. 127, 107713 https://doi.org/10.1016/j.ecolind.2021.107713.
Taylor, D.I., Schiel, D.R., 2010. Algal populations controlled by fish herbivory across a wave exposure gradient on southern temperate shores. Ecology 91 (1), 201–211. https://doi.org/10.1890/08-1512.1.
Thrush, S.F., Hewitt, J.E., Gibbs, M., Lundquist, C., Norkko, A., 2006. Functional role of large organisms in intertidal communities: community effects and ecosystem function. Ecosystems 9 (6), 1029–1040. https://doi.org/10.1007/s10021-005-0068-8.
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. Biol. Sci. 284 (1852) https://doi.org/10.1098/rspb.2016.2861.
Thrush, S.F., Hewitt, J.E., Norkko, A., Nicholls, P.E., Funnell, G.A., Ellis, J.I., 2003. Habitat change in estuaries: predicting broad-scale responses of intertidal macrofauna to sediment mud content. Mar. Ecol. Prog. Ser. 263 (December), 101–112. https://doi.org/10.3354/meps263101.
Törnroos, A., Bonsdorff, E., 2012. Developing the multitrait concept for functional diversity: lessons from a system rich in functions but poor in species. Ecol. Appl. 22 (8), 2221–2236. https://doi.org/10.1890/11-2042.1.
Törnroos, A., Nordström, M.C., Bonsdorff, E., 2013. Coastal habitats as surrogates for taxonomic, functional and trophic structures of benthic faunal communities. PLoS One 8 (10), 1–14. https://doi.org/10.1371/journal.pone.0078910.
Torres, R., Barton, E.D., 2006. Onset and development of the Iberian poleward flow along the Galician coast. Continent. Shelf Res. 26 (10), 1134–1153. https://doi.org/10.1016/j.csr.2006.03.009.
Tyler, C.L., Kowalewski, M., 2018. Data Descriptor: Regional Surveys of Macrobenthic Shelf Invertebrate Communities in Onslow Bay, vols. 1–8. North Carolina, U.S.A. Scientific Data. https://doi.org/10.1038/sdata.2018.54.
Vadas, R., Wright, W., Miller, S., 1990. Recruitment of Ascophyllum nodosum: wave action as a source of mortality. Mar. Ecol. Prog. Ser. 61 (September), 263–272. https://doi.org/10.3354/meps061263.
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. Indicat. 20, 121–133. https://doi.org/10.1016/j.ecolind.2012.02.004.
van der Wal, D., Lambert, G.I., Ysebaert, T., Plancke, Y.M.G., Herman, P.M.J., 2017. Hydrodynamic conditioning of diversity and functional traits in subtidal estuarine macrozoobenthic communities. Estuar. Coast Shelf Sci. 197, 80–92. https://doi.org/10.1016/j.ecss.2017.08.012.
Veiga, P., Rubal, M., Vieira, R., Arenas, F., Sousa-Pinto, I., 2013. Spatial variability in intertidal macroalgal assemblages on the North Portuguese coast: consistence between species and functional group approaches. Helgol. Mar. Res. 67 (1), 191–201. https://doi.org/10.1007/s10152-012-0315-2.
Veiga, P., Redondo, W., Sousa-Pinto, I., Rubal, M., 2017. Relationship between structure of macrobenthic assemblages and environmental variables in shallow sublittoral soft bottoms. Mar. Environ. Res. 129, 396–407. https://doi.org/10.1016/j.marenvres.2017.07.002.
Veiga, P., Torres, A.C., Aneiros, F., Sousa-Pinto, I., Troncoso, J.S., Rubal, M., 2016. Consistent patterns of variation in macrobenthic assemblages and environmental variables over multiple spatial scales using taxonomic and functional approaches. Mar. Environ. Res. 120, 191–201. https://doi.org/10.1016/j.marenvres.2016.08.011.
Vergés, A., Alcoverro, T., Ballesteros, E., 2009. Role of fish herbivory in structuring the vertical distribution of canopy algae Cystoseira spp. in the Mediterranean Sea. Mar. Ecol. Prog. Ser. 375 (February), 1–11. https://doi.org/10.3354/meps07778.
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. https://doi.org/10.1890/07-1206.1.
Vitorino, J., Oliveira, A., Jouanneau, J.M., Drago, T., 2002. Winter dynamics on the northern Portuguese shelf. Part 2: bottom boundary layers and sediment dispersal. Prog. Oceanogr. 52 (2–4), 155–170. https://doi.org/10.1016/S0079-6611(02)00004-6.
Ward, D., Thomas-Melbourne, J., Pecl, G.T., Evans, K., Green, M., McCormack, P.C., Novaglio, C., Trebilco, R., Bax, N., Brasier, M.J., Cavan, E.L., Edgar, G., Hunt, H.L., Jansen, J., Jones, R., Lea, M.-A., Makomere, R., Mull, C., Semmens, J.M., et al., 2022. Safeguarding marine life: conservation of biodiversity and ecosystems. Rev. Fish Biol. Fish. 32 (1), 65–100. https://doi.org/10.1007/s11160-022-09700-3.
Weigel, B., Blenckner, T., Bonsdorff, E., 2016. Maintained functional diversity in benthic communities in spite of diverging functional identities. Oikos 125 (10), 1421–1433. https://doi.org/10.1111/oik.02894.
Wetzel, M.A., Von Der Ohe, P.C., Manz, W., Koop, J.H.E., Wahrendorf, D.S., 2012. The ecological quality status of the Elbe estuary. A comparative approach on different benthic biotic indices applied to a highly modified estuary. Ecol. Indicat. 19, 118–129. https://doi.org/10.1016/j.ecolind.2011.08.007, 2012.
Wildish, D., Kristmanson, D., 1997. Benthic Suspension Feeders and Flow. Cambridge University Press. https://doi.org/10.1017/CBO9780511529894.
Wilkinson, C.R., Evans, E., 1989. Sponge distribution across Davies Reef, Great Barrier Reef, relative to location, depth, and water movement. Coral Reefs 8 (1), 1–7. https://doi.org/10.1007/BF00304685.
Wirtz, P., Debelius, H., 2003. Mediterranean and Atlantic Inverterbrate Guide. ConchBooks. https://doi.org/10.1651/s-2665.1.
Wong, M.C., Dowd, M., 2015. Patterns in taxonomic and functional diversity of macrobenthic invertebrates across seagrass habitats: a case study in atlantic Canada. Estuar. Coast. https://doi.org/10.1007/s12237-015-9967-x.
Wooster, W.S., Bakun, A., McLain, D.R., 1976. The seasonal upwelling cycle along the eastern boundary of the North Atlantic. J. Mar. Res. 34 (2).
World Register of Marine Species, 2023. WoRMS editorial board. https://doi.org/10.14284/170.
Xu, Y., Yu, F., Li, X., Ma, L., Dong, D., Kou, Q., Sui, J., Gan, Z., Gong, L., Yang, M., Wang, Y., Sun, Y., Wang, J., Wang, H., 2018. Spatiotemporal patterns of the macrofaunal community structure in the east China sea, off the coast of zhejiang, China, and the impact of the kuroshio branch current. PLoS One 13 (1), 1–17. https://doi.org/10.1371/journal.pone.0192023.