



Functional structure and diversity of marine benthos reflect food availability and quality, as evidenced by isotopic diversity

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Abstract

Organic matter (OM) resources shape not only the trophic diversity of benthic communities but also the diversity of benthic functional traits. The resulting community structure has a direct effect on many ecosystem processes and functions. Still, the relationship between functional diversity of marine benthos and its trophic diversity in response to the variability of food remains poorly investigated. To explore this relationship we focused on the assessment of various facets of macrobenthic diversity in two temperate coastal areas (southern Baltic Sea) characterized by similar species pool and habitat properties but different OM sources and supplies. We also identified spatio-temporal patterns of functional structure and assessed, which OM properties had the strongest influence on benthic communities. In our study, functional space dispersion followed isotopic space dispersion, reflecting the positive relationship between food variability and ecological functions of benthic communities. Moreover, functional structure in shallow areas was more location-specific in comparison to deeper areas, and this was significantly related to OM parameters. Higher OM variability close to the river mouth prevented the community from becoming dominated by one specialized species, whereas limited OM supply at shallow open coast lowered the diversity by enabling stronger competitor to dominate the community. In more offshore areas, local OM variability ceased and hence, communities tended to reflect similar trophic and functional patterns. Our study demonstrates that functional and isotopic diversity approaches can be effectively combined to better understand mechanisms driving benthic community structure and confirm that greater variability in OM supply increases diversity of benthic communities.

Benthic fauna is involved in multiple ecosystem processes and functions, including modification of physical habitat (De Smet et al. 2015; Donadi et al. 2015), influence on biogeochemical cycles (e.g., Karlson et al. 2007), or energy flow in marine food webs (Griffiths et al. 2017). However, the role that benthos plays in ecosystems depends on its overall activity and diversity of communities (Song et al. 2014). To

improve our understanding of the links between benthos and ecosystem functioning the knowledge about processes influencing the assembly (i.e., formation) and diversity of benthic communities is crucial (Beauchard et al. 2017).

A good measure of ecological functions of benthos is functional diversity (the diversity of ecological, behavioral, and morphological characteristics of species, i.e., biological traits), as it describes the distribution and range of organism's activities and roles in communities and ecosystems (Petchev and Gaston 2006). Functional diversity is considered a principal driver of ecosystem processes and a good tool for estimations of ecosystem vulnerability and resilience (Solan et al. 2004). It can also be used to investigate changes in benthic community structure and functioning in time and space (Villéger et al. 2012), including those driven by human stressors (Oug et al. 2012; Gusmao et al. 2016).

Trophic diversity studies, on the other hand, focus on the diversity of trophic links and interactions in food webs. Thanks to the use of stable isotope analysis, trophic diversity research allows to track the flow of energy and matter through food webs (Layman et al. 2007) and therefore, helps to understand how benthic communities utilize different food

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Additional Supporting Information may be found in the online version of this article.

Author Contribution Statement: M. Szczepanek involved in conceptualization, formal analysis, funding acquisition, investigation, visualization, and writing—original draft preparation. M. Silberberger involved in conceptualization, investigation, and writing—review and editing. M. Kędra involved in conceptualization, funding acquisition (supporting), and writing—review and editing.

resources (e.g., Włodarska-Kowalczyk et al. 2019; Szczepanek et al. 2022). While it was demonstrated that increasing biodiversity positively influences the complexity of benthic food webs (Sokołowski et al. 2012), knowledge on how basal resources influence benthic ecosystem functions and services through the impact on benthic communities is still scarce (Hudson et al. 2003; Campanyà-Llovet et al. 2017).

Benthic consumers, such as suspension- and deposit-feeders, create the lower part of the food web as they rely on primary food sources in the form of fresh or decomposed organic matter (OM) from various origins (Hoffman et al. 2008; Pardo et al. 2023). It is well recognized that the quantity and quality of OM are some of the most important factors shaping benthic community structure (Dauwe et al. 1998; Moore et al. 2004; Campanyà-Llovet et al. 2017). OM does not only shape the set of functional traits in a particular habitat (e.g., morphology, foraging behavior, and feeding activity) but also the diversity of trophic interactions in food webs (Keddy 1991; Moore et al. 2004). Still, the relationship between functional diversity of marine benthos and its trophic (isotopic) diversity in response to the variability of food remains poorly investigated.

During the last two decades, many ecological indicators have been developed to properly assess multiple facets of functional diversity (Villéger et al. 2008; Laliberté and Legendre 2010) and the same approaches have been transferred to assess isotopic diversity (Cucherousset and Villéger 2015; Rigole et al. 2015). So far, however, only a few studies, concentrated mainly on high latitudes, combined both functional and isotopic approaches to study the life history and diversity of benthic communities (Włodarska-Kowalczyk et al. 2019; Ehrman et al. 2022). Benthic communities from polar and temperate areas are, however, driven by different regimes of food supply resulting from different seasonality and primary production patterns (Kędra et al. 2015; Tamelander et al. 2017). Temperate coastal areas experience also inputs from terrestrial and riparian vegetation and human-induced inputs from agriculture, deforestation, and wastewater treatments, among others (Maksymowska et al. 2000; Tamelander et al. 2017; Szczepanek et al. 2021). Therefore, in these areas, higher spatio-temporal variability of benthic isotopic diversity should be expected, with an unknown relationship to the functional diversity of fauna.

The main aim of this study is to investigate: (1) the spatio-temporal relationship between the trophic (isotopic) and functional diversity of benthic communities and (2) the influence of food source variability on the functional structure of benthos in temperate coastal areas. To address these questions, we studied different facets of benthic diversity within two coastal areas of the southern Baltic Sea characterized by similar species pool and habitat properties but by different OM sources and supplies. We hypothesize that in the region with a smaller, mainly autochthonous supply of OM (open coast of Poland) isotopic and functional diversity are

low. In contrast, in the region with more abundant and diverse OM sources due to the riverine input (Vistula River prodelta), we expect benthic communities to show greater isotopic diversity and consequently, a higher diversity of functional traits.

Materials and methods

Study area

Shallow areas of the southern Baltic Sea along the Polish seashore can be divided into the open coast, which receives primarily autochthonous OM, and the Gulf of Gdańsk, which is greatly supplied with the anthropogenically impacted Vistula River waters (Andrulewicz et al. 2004). Additionally, strong seasonal variation in primary production is typical in those areas (Tamelander et al. 2017; Szczepanek et al. 2021). Both the open coast of Poland and the Gulf of Gdańsk experience strong bottom currents with velocities exceeding 0.5 m s^{-1} under storm conditions (Sokolov and Chubarenko 2012; Cieślakiewicz et al. 2017). The water column is characterized by similar salinity and temperature profiles (Gic-Grusza et al. 2009). Medium and fine-grained sands dominate down to 60–90 m depth (Gic-Grusza et al. 2009). The macrobenthic species pool is similar throughout the whole Baltic Proper (Zettler et al. 2014; Gogina et al. 2016), and oxygen conditions do not affect community structure in shallow habitats (Kendzierska 2017).

Field sampling

Two sampling locations were selected for the study (Fig. 1): the open coast of Poland (ML) and the prodelta of Vistula River (MW). Each location was sampled at two transects along the 15 and 30 m isobaths, and at each depth transect three stations were sampled (Supporting Information Table S1). Southwesterly and westerly winds are pronounced in the southern part of the Baltic Sea and force water mass to the east (Grelowski and Wojewódzki 1996). Thus, stations located in the Vistula prodelta were arranged to start from the river mouth to the east in order to cover the potential local variability of OM transported by the river plume. Sampling was conducted on board of s/y Oceania during January 2019 (winter) and October 2019 (autumn) to account for seasonal variability in OM properties. We assumed that samples from January would allow detection of the effect of winter slowdown manifested by starvation and interruption of the productive period, whereas samples from October (autumn) would allow detection of the highest peak of secondary production as well as isotopic signals of fresh and abundant phytodetritus from the late summer bloom (Włodarska-Kowalczyk et al. 2016; Szczepanek et al. 2021, 2022).

Near bottom water samples for the analyses of particulate organic matter (POM) and phytopigments (chlorophyll *a* (Chl *a*) and phaeophytin) were taken by Niskin bottle. Water samples for POM were filtered through the precombusted and pre-

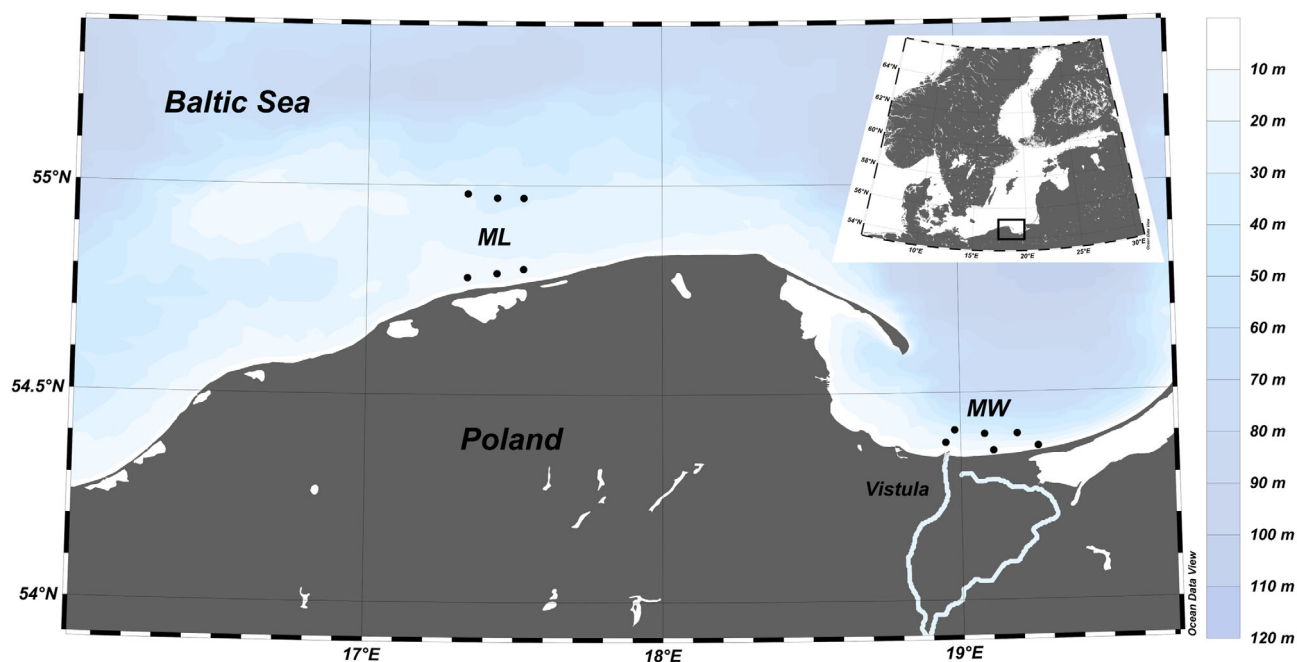


Fig. 1. Map of the study region illustrating sampling stations at the open coast of Poland (ML) and Vistula River prodelta (MW). Baltic Sea in the insert.

eighed Whatman GF/F filters (\varnothing 47 mm; pore size: 0.7 μm), which were immediately frozen at -20°C until laboratory analyses. Water samples for Chl *a* and phaeophytin (phaeo) were filtered through Whatman GF/F filters (\varnothing 25 mm; pore size: 0.7 μm) in the dark and filters were frozen at -80°C .

At each station, surface sediment samples were taken for the analyses of phytopygments (1 cm depth), sedimentary organic matter (SOM), and granulometry (5 cm depth) with the use of box corer. Sediments for phytopygments and other sediment samples were frozen at -80°C and -20°C , respectively.

Sediment biological samples from each station (three replicates for quantitative taxonomic analysis and an additional one for isotopic analyses) were collected by van Veen Grab (0.1 m^2 sampling area) and washed over a 0.5 mm mesh size sieve. Faunal samples for taxonomic analysis were fixed in a buffered 4% formaldehyde solution. All found species from the additional grab were sorted out immediately after sampling (in the amount necessary for stable isotope analysis) and kept alive for ~ 24 h in filtered seawater to allow for gut clearance. Isotopic samples were frozen at -80°C until analysis.

Laboratory analyses

Phytopygments

Chl *a* and phaeophytin (phaeo) concentrations in bottom water (filters) and surface sediment samples were quantified fluorimetrically following the Environmental Protection Agency method 445.0 (Arar and Collins 1997). Defrosted filters and freeze-dried, homogenized sediments (~ 1 g DW) were extracted in 10 mL of 95% acetone for 20–24 h at 4°C

and centrifuged (3000 rpm for 2 min). The supernatant was then analyzed with a Trilogy[®] fluorimeter (Turner Designs) before and after acidification with 100 μL of 0.1 M HCl (Arar and Collins 1997).

Stable isotopes

Analyses for organic carbon (C_{org}) and total nitrogen (N_{tot}) and their stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in POM, SOM, and animal tissue samples were done in an Elemental Analyzer Flash EA 1112 Series combined with the Isotopic Ratio Mass Spectrometer IRMS Delta V Advantage (Thermo Electron Corp., Germany). Freeze-dried and homogenized samples were weighed into silver capsules (about 35–45 mg, 75–80 mg, and 1 mg for POM, SOM, and animal tissue respectively), soaked with 2 M HCl to remove carbonates, and dried at 60°C for 24 h (Kuliński et al. 2014). Following findings of Silberberger et al. (2021), lipids were not removed from the samples. C_{org} and N_{tot} measurements were calibrated against certified reference materials (marine sediments) provided by HEKATEch GmbH (Germany). The results of $\delta^{13}\text{C}$ were calibrated against IAEA standards: CO-8 and USGS40, and $\delta^{15}\text{N}$ results against N-1 and USGS40. Stable isotope ratios are given in the conventional delta notation, i.e., vs. Vienna Pee Dee Belemnite for ^{13}C and vs. air for ^{15}N as parts per thousand (‰).

Granulometry

Sediment samples for granulometric analysis were dried (48 h, 60°C) and sieved with a shaker through a set of standard test sieves (mesh diameters: 2, 1, 0.5, 0.25, 0.125, and 0.063 mm). Sediment parameters were calculated using the

method of Folk and Ward (1957) in the program GRADISTAT 8.0 (Blott and Pye 2001).

Macrofauna

Macrofauna from grab samples was identified to the lowest possible taxonomic level (preferably species) under a stereomicroscope, counted, and wet-weighed (with 0.1 mg accuracy).

Data processing

Taxonomic database

Nematodes and ostracods, as well as six macrobenthic species that occurred only once in the whole data set, and for which isotopic data were not available, were excluded from the analysis. Several taxa that could not be identified to species level during collection of isotopic samples were pooled into families, i.e., two Spionidae (*Streblospio shrubsoli* and *Pygospio elegans*), two Hydrobiidae (*Ecrobia ventrosa* and *Peringia ulvae*), and three Corophiidae (*Corophium volutator*, *Corophium multisetosum*, and *Chelicorophium curvispinum*). The resulting database contained 18 taxa in total (Supporting Information Fig. S1), which well represented macrobenthic species pool occurring in both regions (own data). In case when stable isotope samples for particular species at a particular station were not available, they were complemented by the mean values from the corresponding sampling depth or different sampling period (Zapata-Hernández et al. 2021). Such cases represented ~ 4.18% of the total biomass of species collected during both sampling campaigns.

Functional traits base

We chose six benthic functional traits related to key components of essential functions provided by coastal ecosystems (Słomińska 2018), namely, carbon storage potential (longevity and maximum size), resource use (feeding type), and animal bioturbation potential (mobility, biomixing, and bio-transport). Each functional trait was divided into specific categories (modalities) into which species could be assigned (Table 1). Information on functional traits of benthic species was obtained from available scientific knowledge published in peer-reviewed papers, or internet databases, e.g., BIOTIC (MarLIN 2006) or WoRMS (WoRMS Editorial Board 2024). In the case where a particular species represented more than one modality within a given functional trait, the fuzzy coding technique with affinity scores was adapted (Chevenet et al. 1994).

Isotopic traits base

To compute isotopic diversity indices, data on stable isotopes of taxa identified at every site (separately from January and October) were adapted into two continuous traits, i.e., $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. To reduce the influence of divergent isotopic baselines occurring between locations (Szczepanek et al. 2021), the whole isotopic dataset was globally scaled between 0 and 1 (Cucherousset and Villéger 2015).

Data analysis

Analysis of OM variability

To test for significant differences in OM and sediment parameters between locations, months, and depths the non-parametric Kruskal–Wallis ANOVA tests on ranks were conducted with the use of rstatix package in R 4.2.1 (R Core Team 2023). In total, seven OM parameters (Chl *a*, phaeo, C_{org} , N_{tot} , $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and Chl *a*/phaeo ratio) were used for the assessment of OM quantity, quality, and origin both in POM and SOM (Supporting Information Table S2). Those parameters included. Chl *a*, phaeo, and C_{org} give information about OM quantity, N_{tot} , and Chl *a*/phaeo ratio inform about OM nutritional quality and freshness, whereas isotopic ratios indicate OM origin (Szczepanek et al. 2021). The N_{tot} was not included in the analyses due to the high correlation with C_{org} both in POM and SOM (Pearson's $R > 0.9$; $p < 0.001$). The tested sediment characteristics included mean grain size and mud content in the sediment.

Analysis of functional structure

The functional structure of benthic communities was summarized using community-weighted means (CWM), i.e., by multiplying the relative biomass of all species exhibiting given modalities within a trait by their standardized fuzzy-coded values (Leps et al. 2006). On the basis of CWMs from each modality, the matrix of Bray–Curtis dissimilarities between pairs of stations and months was calculated. On this resemblance, PERMANOVA tests were conducted to check for significant differences between locations, months, and depths, as well as crossed factors (if significant). Additionally, to find the part of the variation in the functional structure that could be explained by OM variability, a distance-based linear model (distLM) was conducted using 12 OM parameters as predictor variables (raw values in Supporting Information Table S2). The distLM was carried out using 9999 permutations with a forward selection procedure and AICc selection criterion. The results from the best-fitted model have been represented by two first axes of the distance-based redundancy analysis (dbRDA). PERMANOVA, distLM, and dbRDA analyses.

Analysis of functional and isotopic diversity

The isotopic and functional diversities were computed using a distance-based multidimensional framework (Villéger et al. 2008; Laliberté and Legendre 2010; Cucherousset and Villéger 2015) with functions available in mFD package (Magneville et al. 2022) in R environment (R Core Team, 2023). Separate multidimensional spaces were calculated based on the pairwise distances of species in the isotopic and trait matrix. Isotopic space was calculated from Euclidean distance, whereas functional space was calculated first by Gower distance, which was then transformed to Euclidean by calculating distances among coordinates from the first five axes of principal coordinate analysis of Gower distances (Laliberté and Legendre 2010; Magneville et al. 2022). Only the first five axes, which explained 93% of variance, were chosen to

Table 1. Functional traits and their modalities used for the analysis of the functional structure of benthic communities in the study area (modified after Stomińska 2018).

Trait	Modality	Abbrev.	Explanation
Maximum size	S	S	Small (1–5 mm)
	SM	SM	Small–medium (5–10 mm)
	M	M	Medium (10–30 mm)
	ML	ML	Medium–large (30–50 mm)
	L	L	Large (> 50 mm)
Longevity	Very short	VS	Very short (< 1 yr)
	Short	Sh	Short (1–2 yr)
	Long	Lo	Long (2–5 yr)
	Very long	VL	Very long (> 5 yr)
Feeding type	Suspension feeder	SUS	Feeds on suspended material
	Surface deposit feeder	SUR	Feeds on surface deposits
	Sub-surface deposit feeder	SUB	Feeds on subsurface deposits
	Gazer/scrapper	GR	Feeds on plants or microphytobenthos
	Predator/scavenger	PR	Feeds on living or dead animals
Mobility	Sedentary	Se	None or temporary movement
	Limited free movement	LM	Movement limited to, e.g., tube or canal
	Freely motile	FM	Moves freely in or on sediment
	Swimming above sediment	SAS	Temporary action
Biomixing	No mixing	NM	No contact with sediment (e.g., lives on elements protruding above the surface)
	Epifaunal biodiffusors	EB	Redistribute fine particles randomly over very short distances along the surface
	Surficial biodiffusors	SB	Mixing activities mostly restricted to the first 5 cm of the sediment
	Deep biodiffusors	DB	Mixing activities reaching below 5 cm in sediment
	Gallery biodiffusors	GB	Excavates, maintains and ventilates tunnels up to tens of cm
Biotransport	Surface deposition	SD	Accretion of suspended organic matter as feces and pseudofeces on the sediment surface
	Surficial transport	ST	Stochastic transport of organic particles through the digestive system
	Upward conveyor	UC	Transport of particles by the gut passage from deep to surface
	Downward conveyor	DC	Transport of particles by the gut passage from surface to depth

compute functional trait spaces according to quality tests proposed by Maire et al. (2015). Representations of isotopic and functional spaces can be found in the Data S1 of this article (Supporting Information Figs. S2 and S3, respectively).

Three indices describing isotopic and functional spaces were computed to describe different complementary facets of isotopic and functional diversities, i.e., dispersion (IDis; FDis), evenness (IEve; FEve), and divergence (IDiv; FDiv) (Villéger et al. 2008; Laliberté and Legendre 2010; Cucherousset and Villéger 2015). Dispersion is a measure of the mean distance of individual species to the centroid of multidimensional space, where the position of the centroid

shifts toward species that are more abundant. Therefore, higher dispersion indicates a greater breadth of isotopic/functional space. Evenness is a measure of the regularity of species abundance distribution in multidimensional space. It tends to be higher in communities where isotopic signals/traits are evenly distributed among species. Divergence is a measure of distinction of abundance distribution, therefore higher divergence indicates that more abundant species represent extreme values, i.e., they are closer to the edges of the multidimensional space (Villéger et al. 2008). Divergence tends to be low when more abundant species represent the most common traits/food sources.

All diversity indices computed in our study accounted for species weighting (Cucherousset and Villéger 2015). We have chosen biomass to weigh the species in assemblages since biomass is directly related to animal metabolism as well as to secondary production. It is thus a more relevant proxy for the functional impact of an individual species within an ecosystem compared to, e.g., density (Rigolet et al. 2015; Gogina and Zettler 2023). During the calculation of indices, the biomass data were standardized between 0 and 1 to represent relative values.

All six diversity indices and additionally absolute species richness (number of species per station) were checked for normality distribution (Shapiro–Wilk test on residuals from linear regression) and homogeneity of variances (Levene's test). Since the conditions have been met, the data were tested for significant differences using univariate ANOVA (ANOVA). ANOVA was conducted with functions implemented in the “rstatix” package in R, using three independent variables, i.e., “location” (ML vs. MW), “month” (January vs. October), and “depth” (15 m vs. 30 m). To assess the strength of the relationship between corresponding pairs of diversity indices, Pearson's *R* correlations were used and the significance of the correlation was checked.

Results

Taxonomic and functional structure

Higher benthic biomass at sampling stations was mostly observed in October compared to January (ranging from 6.8 to 414.9 g m⁻² and from 3.4 to 72.4 g m⁻², respectively), with larger temporal variation at shallow stations (Supporting Information Table S1). Benthic communities were dominated by bivalves (*Cerastoderma glaucum*, *Macoma balthica*, and *Mya arenaria*), mud snails (Hydrobiidae) and large polychaetes *Hediste diversicolor* and *Marenzelleria* spp., which represented higher biomass in comparison to other abundant species like oligochaetes, spionids, or amphipods also observed in the samples (Supporting Information Fig. S1). Species richness did not differ between locations, as well as between sampling months, however, significantly higher species number was observed at deeper stations compared to shallow ones (ANOVA, *p* = 0.002).

Functional structure (CWM) at shallow stations (15 m) from the open coast (ML) was the most distinct from any other group (Fig. 2; Supporting Information Fig. S4) and characterized by the dominance of one modality in each functional trait because of very high biomass of medium-sized surface biodiffusor and suspension-feeder—*C. glaucum*. At shallow stations from the Vistula prodelta (MW), the weight of modalities was more evenly distributed within traits (Fig. 2; Supporting Information Fig. S4). Also in this group of stations, a higher share of gallery builders and deep biodiffusors was observed, as well as of large-sized animals in comparison to deeper stations, resulting from higher

biomass of *H. diversicolor* and the large-bodied clam *M. arenaria*. Deeper stations in both locations were dominated by *M. balthica*, and the functional flexibility of this species considerably modified benthic functional structure and diversity.

Both location and depth had a significant effect on the functional structure of benthic communities in the study area (PERMANOVA; *p* = 0.001; Table 2). Nonetheless, the pair-wise comparison did not detect significant differences between deeper stations from both locations (pseudo-*F* = 1.097; *p* = 0.267). This implies that differences between locations resulted from factors affecting mostly the shallow stations. The functional structure did not show any significant seasonal changes.

OM influence on functional structure

We detected significant temporal variability of POM parameters (Chl *a*, phaeo, Chl *a*/phaeo, and C_{org}) in the study area (Table 3; Supporting Information Table S2) with higher quantity and quality of suspended food available for macrobenthos in October compared to January. Regardless of location, δ¹³C and δ¹⁵N in bottom waters significantly differed between depths, with higher δ¹³C and lower δ¹⁵N at deeper sites, indicating different OM composition and/or status of microbial degradation. Additionally, significantly lower C_{org} values were observed in bottom waters from deeper sites.

Significant differences in SOM parameters were observed between study locations (phaeo, Chl *a*/phaeo, C_{org}, δ¹³C, and δ¹⁵N), indicating a higher concentration of refractory and/or riverine OM in the sediments from Vistula prodelta in comparison to sediments from the open coast. Additionally, higher SOM quality was noted at shallow sites, which resulted from complex variability of Chl *a* and phaeo concentrations in the sediment (Supporting Information Table S2). Importantly, although the percentage of mud content in sediments significantly differed between locations (Kruskal–Wallis test, *p* = 0.001), the mean grain size did not differ between sampled locations, depths, or months (Table 3).

The distLM distinguished three OM variables, i.e., Chl *a*/phaeo in SOM as well as C_{org} and δ¹³C in POM responsible for variation in the community functional structure (Table 4). The first two axes of dbRDA explained 57.1% of the total variation in the functional structure, visually distinguishing the group of samples from shallow and deep stations as well as the group from shallow stations of the open coast from the rest of the points (Fig. 3), thereby confirming results of PERMANOVA (Table 2).

Functional and isotopic diversity

The highest FDis was observed at shallow stations from the Vistula prodelta (Fig. 4). Although isotopic dispersion (IDis) was relatively low in comparison to FDis, both indices followed the

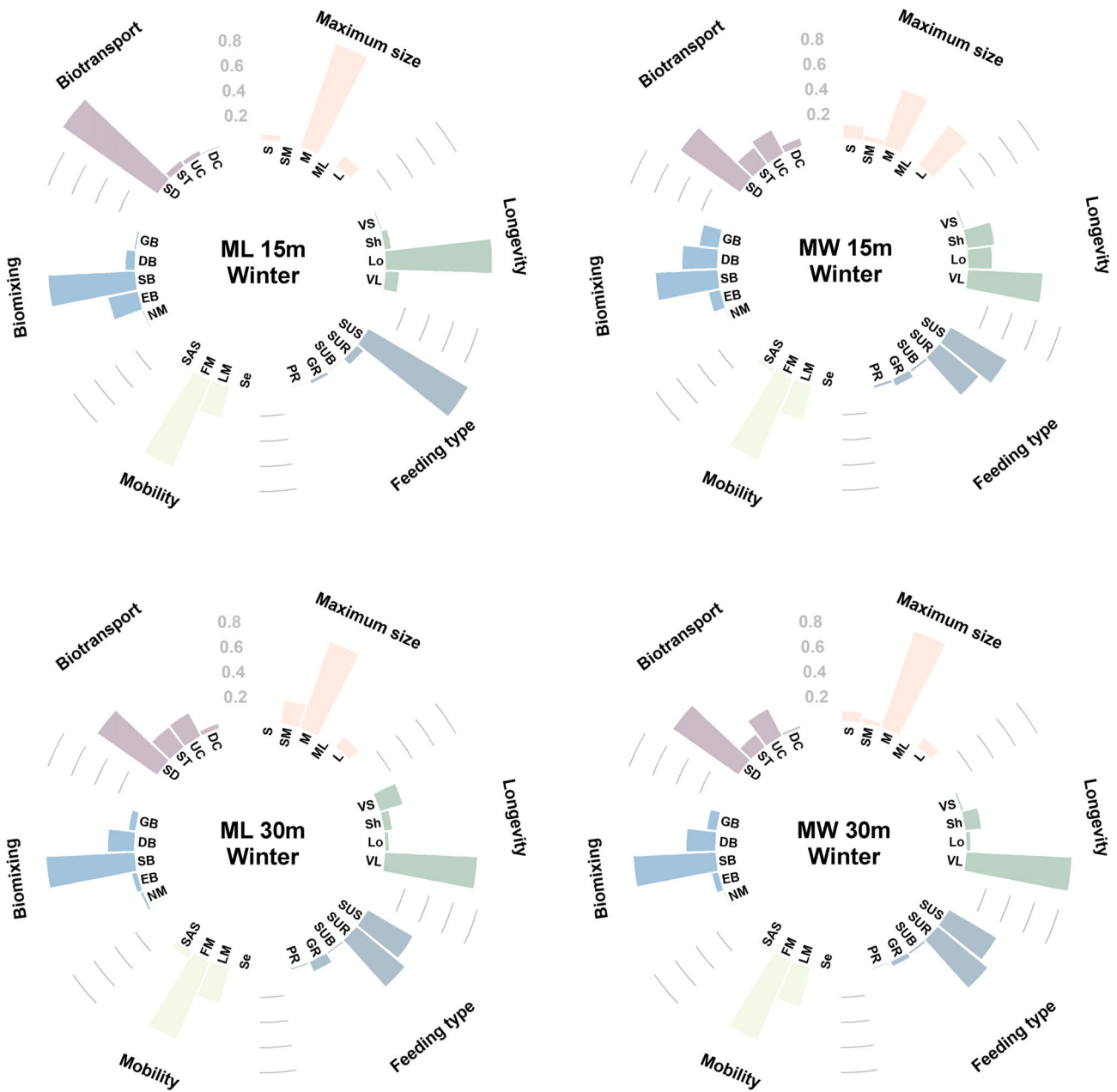


Fig. 2. CWMs of benthic communities' functional structure from the open coast of Poland (ML) and Vistula River prodelta (MW) at different depths in January 2019. Results for October 2019 are shown in Supporting Information Fig. S4. For abbreviations of modalities see Table 1.

same spatial pattern and were significantly correlated (Supporting Information Fig. S6; $R = 0.75$, $p < 0.001$). Functional evenness (FEve) was significantly lower at shallow stations in both locations in comparison to deeper ones (ANOVA, $p = 0.001$), whereas functional divergence (FDiv) was slightly but significantly lower at the open coast compared to Vistula prodelta (ANOVA, $p = 0.033$) (Fig. 4; Table 5). Neither isotopic evenness (IEve) nor isotopic divergence (IDiv) differed on a spatio-temporal scale, and consequently, they were not

correlated to the corresponding functional indices. None of the indices showed significant temporal differences (Table 5).

Discussion

We combined both multivariate analyses of community functional structure and multidimensional diversity measures to (1) assess the relationship between trophic (isotopic) diversity of marine benthos with its functional diversity and (2) find

Table 2. Results of multivariate PERMANOVA tests for differences in functional structure (CWM) of benthic communities from the study area - open coast of Poland (ML) and Vistula prodelta (MW). The main test was conducted among locations, months, and depths. Pair-wise tests were conducted for significant interactions between factors of location and depth.

Main test	Factor	Pseudo-F	p
Df = 16	Location (lo)	14.608	**
	Mo (Mo)	1.243	ns
	Depth (De)	23.336	**
	Lo × Mo	1.819	ns
	Lo × De	17.622	**
	Mo × De	0.229	ns

Pair-wise tests	Factor (groups)	t	p
Df = 10	15 m (ML; MW)	6.198	**
	30 m (ML; MW)	1.097	ns
	ML (15; 30)	5.462	**
	MW (15; 30)	3.160	**

ns, not significant.

* $p < 0.05$;

** $p < 0.01$;

*** $p < 0.001$.

how OM properties influence benthic functional structure. Our results show that dynamic environmental conditions strongly influenced benthic community structure in shallow

waters, though, it was the quantity and quality of OM that shaped functional patterns the most. In more offshore areas, local variability of OM and hydrological conditions (temperature and salinity) ceased in favor of the open waters, and hence, communities tended to reflect similar trophic and functional patterns related to the quantity of degraded OM.

Taxonomic and functional structure

The taxonomic composition in the study area was in agreement with the previously described division into shallow and more offshore communities that was observed in the southern Baltic Sea (Gic-Grusza et al. 2009; Gogina et al. 2016; Włodarska-Kowalczyk et al. 2016; Miernik et al. 2023). We noticed three functionally distinct communities, one present at both deeper sites, and two different for each shallow site (Table 2). Our modeling results support that this visually clear distinction of functional structure with depth could be explained by the variability of OM properties (Table 4; Fig. 3). Shallow sites, due to different food sources and availability (reflected in C_{org} concentrations and lower $\delta^{13}C$ values, Supporting Information Table S2) were distinct both from each other and from deeper sites from corresponding locations. This functional distinction faded with increasing depth, where OM sources were more stable throughout the year due to the dominance of marine-originating OM and higher detrital pool in sediments (this study; Silberberger et al. 2021; Szczepanek et al. 2022).

Similar depth-related patterns of multivariate macrobenthic community structure were previously observed in the Vistula prodelta (Włodarska-Kowalczyk et al. 2016). The overall, relatively

Table 3. Results of non-parametric Kruskal–Wallis ANOVA test on ranks for differences in OM and sediment characteristics between locations, months, and depths in the study area ($n = 24$, $df = 1$).

Source	Variable	Location		Month		Depth	
		F	p	F	p	F	p
POM	Chl a/phaeo	0.04	ns	17.30	***	0.10	ns
	Chl a	0.75	ns	9.40	**	1.77	ns
	Phaeo	1.27	ns	15.00	***	2.08	ns
	C_{org}	0.04	ns	12.10	***	4.49	*
	$\delta^{13}C$	3.20	ns	3.63	ns	5.47	*
	$\delta^{15}N$	1.76	ns	2.61	ns	9.72	**
SOM	Chl a/phaeo	6.03	**	0.14	ns	5.75	*
	Chl a	3.31	ns	0.48	ns	0.44	ns
	Phaeo	11.00	**	0.21	ns	1.61	ns
	C_{org}	12.80	***	0.99	ns	1.90	ns
	$\delta^{13}C$	9.36	**	2.43	ns	1.08	ns
	$\delta^{15}N$	9.01	**	0.21	ns	0.21	ns
Sediment	% Mud content	11.60	**	0.61	ns	2.08	ns
	Mean grain size	0.33	ns	0.00	ns	0.40	ns

POM, particulate suspended organic matter; SOM, particulate sedimentary organic matter; ns, not significant.

* $p < 0.05$;

** $p < 0.01$;

*** $p < 0.001$.

Table 4. Results of the distLM based on forward selection of organic matter (POM and SOM) parameters explaining variation in the functional structure of benthic communities in the study area.

Source	Marginal tests			
	(res. df = 22)	Pseudo-F	p	Prop.
POM	Chl <i>a</i> /phaeo	0.21	ns	0.01
	Chl <i>a</i>	1.21	ns	0.05
	Phaeo	0.64	ns	0.03
	C _{org}	3.02	*	0.12
	δ ¹³ C	2.04	ns	0.08
	δ ¹⁵ N	1.01	ns	0.04
SOM	Chl <i>a</i> /phaeo	17.08	**	0.44
	Chl <i>a</i>	0.64	ns	0.03
	Phaeo	1.99	ns	0.08
	C _{org}	2.82	ns	0.11
	δ ¹³ C	2.53	ns	0.10
	δ ¹⁵ N	4.60	ns	0.17
Sequential tests				
SOM	Chl <i>a</i> /phaeo (res. df = 22)	17.08	**	0.44
POM	δ ¹³ C (res. df = 21)	3.36	*	0.08
POM	C _{org} (res. df = 20)	3.47	*	0.07

POM, particulate suspended organic matter; SOM, particulate sedimentary organic matter; ns, not significant.

* $p < 0.05$;

** $p < 0.01$;

*** $p < 0.001$.

high taxonomic diversity in comparison to the poor disturbed community at direct river outflow followed the pattern of OM quantity and quality, decreasing with increasing distance from the river mouth (Włodarska-Kowalczyk et al. 2016). Gogina and Zettler (2023) stated that in the southwest part of the Baltic Sea, depth, as a cumulative predictor of OM quantity and quality, was one of the main factors determining benthic community structure. Szczepanek et al. (2022) suggested that at greater depths of the Vistula mouth, preferential sediment structure and lower competition for more nutritious food might lead to a community structure dominated by *M. balthica*. A similar rule may be true for the offshore site from the open coast.

Previous studies have shown that at the open Polish coast, high-quality fresh OM supply from intensive spring bloom may be preferentially consumed by suspension-feeders (Lessin et al. 2019; Szczepanek et al. 2021). A low amount of food in unstable sandy sediments probably prevents the occurrence of larger deposit feeders and omnivores (Dauwe et al. 1998; Szczepanek et al. 2021), which additionally lowers resource competition. Moreover, many species of bivalves, including *C. glaucum*, can store energy and nutrient reserves as an adaptation to fluctuations in food supply (Lovvorn et al. 2005; Karray et al. 2015). All these conditions suggest that the high biomass of *C. glaucum* (Supporting Information

Fig. S1) and its importance to the functional structure at shallow open coast results from a limited supply of OM (even though highly nutritious), as well as from low detrital matter accumulation due to bottom erosion and resuspension (Emeis et al. 2002).

Role of OM variability

Certainly, the dominance of *C. glaucum* has largely impoverished the IDis and diminished the functional diversity and structure of the community from the shallow open coast. Inversely, in the Vistula River vicinity, high seasonal variability of OM supply (this study; Włodarska-Kowalczyk et al. 2016; Szczepanek et al. 2021, 2022) resulted in the increase of both isotopic and FDis of benthos. One of the early studies by Dauwe et al. (1998) showed that different benthic feeding groups were associated with sediments characterized by different quantities and quality of OM in the North Sea. Coarse sediments with low but highly labile content of OM were characterized by a poor community largely dominated by surface-feeding *Echinocardium cordatum*, whereas a frontal area with high sedimentation of partly degraded OM was characterized by the most abundant and functionally diverse community (Dauwe et al. 1998). Wieking and Kröncke (2005) also found that stations with the unstable, highly heterogeneous composition of OM represented relatively higher benthic diversity in comparison to sites with a more stable OM supply. Similarly, in the marine ecosystem of Rapa Nui (Easter Island) reef-associated fauna (invertebrates and fishes), which exploited more variable food resources than pelagic fishes, also showed higher trophic diversity (Zapata-Hernández et al. 2021). Our results clearly support the above-mentioned findings.

However, such a clear relationship between isotopic and functional diversity was not found in previous comparisons based on multidimensional spaces (Włodarska-Kowalczyk et al. 2019; Ehrman et al. 2022). Włodarska-Kowalczyk et al. (2019) found that in a harsh, glacially impacted environment characterized by low diversity, benthic communities tended to exploit the range of food resources compared to more functionally diverse communities from less impacted area. Their assumption that higher functional diversity would lead to greater partitioning of trophic resources was however not confirmed. Similarly, functional and isotopic diversities within two contiguous Arctic shelves showed distinct spatial patterns related to local-scale habitat filters, and no differences in isotopic space were observed between the shelves (Ehrman et al. 2022). Based on these findings, it can be concluded that it is not the functional diversity that increases the trophic niche of consumers, but on the contrary, a more diverse food base increases the diversity of benthic functions.

Isotopic and functional niches

Our results clearly indicate that functional trait dispersion (FDis) was interdependent with its isotopic counterpart (IDis)

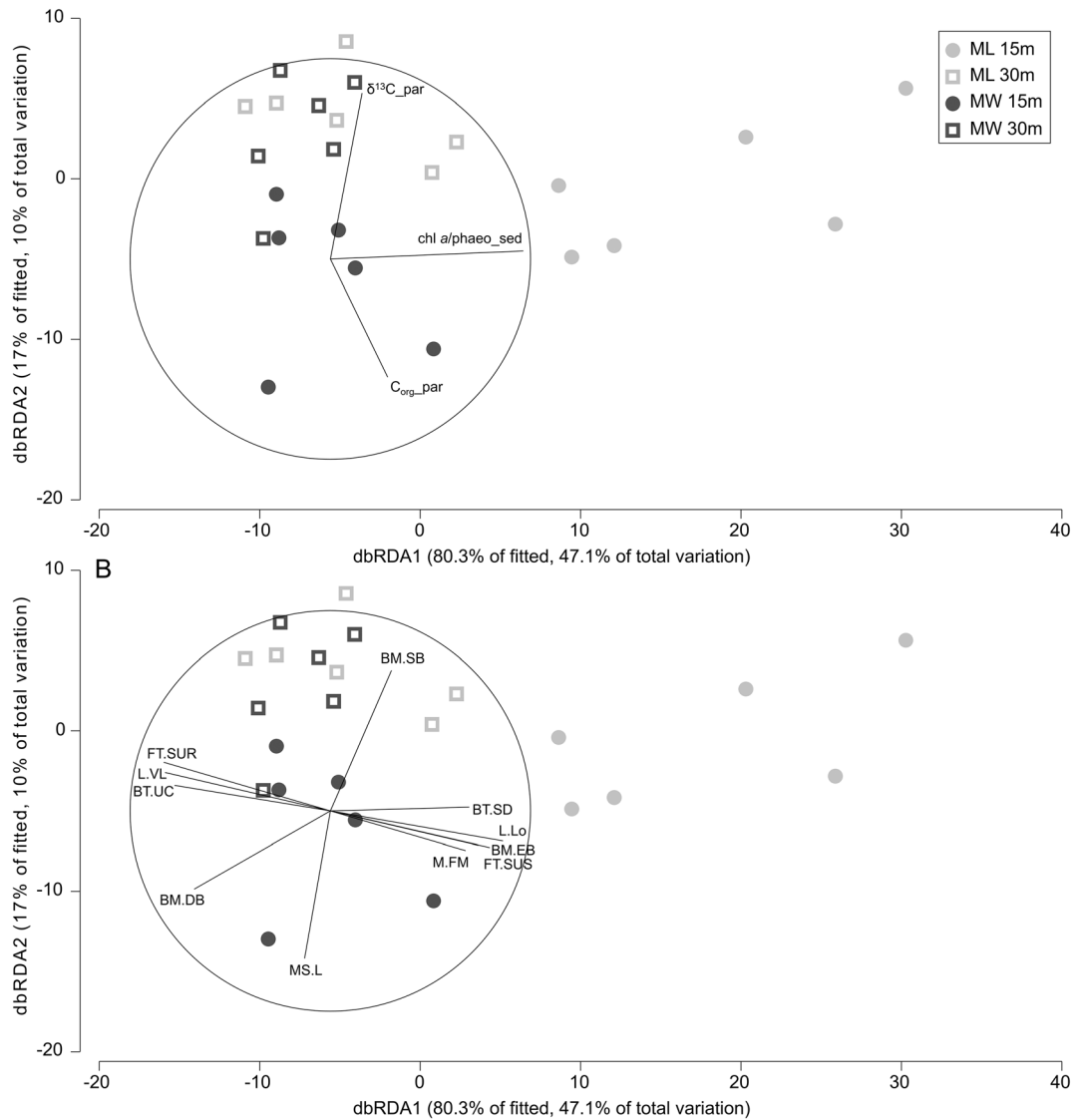


Fig. 3. dbRDA of benthic functional structure based on the distLM—Table 4). Top panel—dbRDA with vectors representing OM parameters responsible for variation; Bottom panel—dbRDA with vectors representing correlated functional modalities ($r > 0.7$). Abbreviations of traits and modalities: BM.DB, biomixing–deep biodiffusors; BM.SB, biomixing–surficial biodiffusors; BT.SD, biotransport–surficial deposition; BT.UC, biotransport–upward conveyor; FT.SUR, feeding type–surface deposit feeder; FT.SUS, feeding type–suspension feeder; L.Lo, longevity–long; L.VL, longevity–very long; M.FM, mobility–freely motile; MS.L, max. size–large.

occupied by communities (Supporting Information Fig. S6), and as previously discussed, both spaces followed the patterns of OM variability. At the open Polish coast, dispersion increased with depth (Fig. 4), following the increasing concentration of degraded OM (phaeo) (Supporting Information Table S2), and therefore the relative decrease in OM quality. In the Vistula prodelta, dispersion increased with the increase of OM sources diversity reflected in seasonal changes in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values driven by the river outflow. We demonstrate that when similar habitat properties are obtained, the spatial variability in OM quantity and quality can greatly explain the structure and diversity of associated benthic communities.

Importantly, we designed this study to analyze the lower part of the food web, consisting mainly of primary consumers. This was confirmed by very low IDIs values, resulting from the low biomass of higher consumers. Besides, low IDIs may also suggest the limited isotopic variability of food sources (Cucherousset and Villéger 2015). This can be explained by the fact that isotopic ratios of OM sources prevalent in the study area, i.e., phytodetritus and riverine debris, fall in a similar range of values (-31 to -19‰ for $\delta^{13}\text{C}$ and 1 to 10‰ for $\delta^{15}\text{N}$; Maksymowska et al. 2000; Sokołowski 2009; Szczepanek et al. 2021). Nonetheless, previous studies have shown that those sources are distinguishable in mixing models (Silberberger

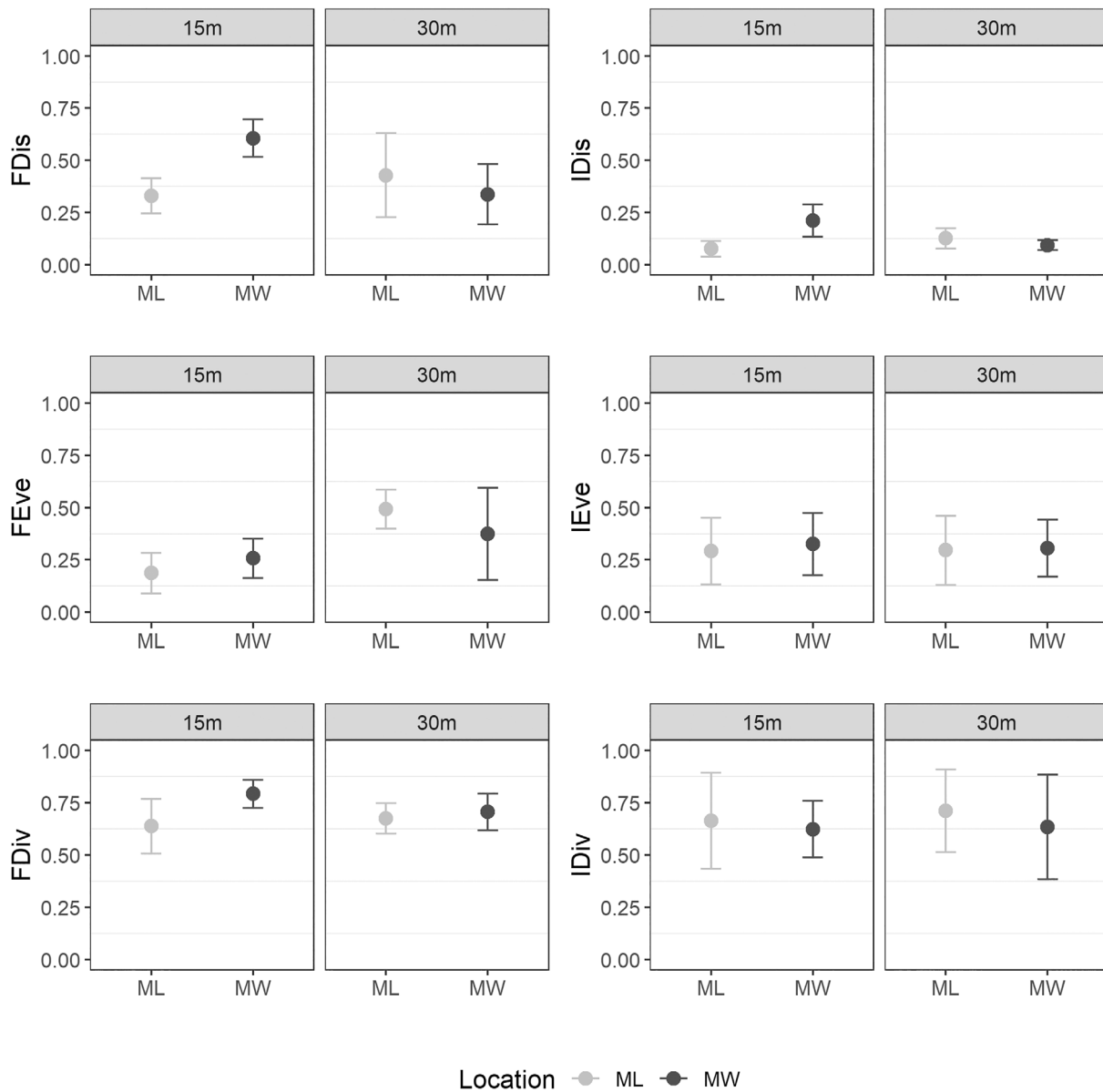


Fig. 4. Indices of functional and isotopic diversity of benthic communities. Indices represent dispersion (FDIs and IDis), evenness (FEve and IEve), and divergence (FDiv and IDiv) of multidimensional functional space and bi-dimensional isotopic space weighted by species biomass. Points represent the mean values from both months ($n = 6$), and vertical lines represent the standard deviation. For details of statistical results see Table 4.

et al. 2021; Szczepanek et al. 2022). Moreover, pulses of riverine OM vary seasonally, what additionally facilitates their recognition.

Consequently, low IEve values in the study area may indicate a high dietary overlap among benthic consumers, resulting from a similar and limited range of resources. The classical ecological theory (MacArthur and Levins 1967) predicts that a high overlap of the feeding niche between species will lead to an increase in competition, which would result in either ecological differentiation or local extinction. It was shown that in communities with high feeding niche overlap dominant species tend to maximize the resource use

through higher feeding plasticity (Lesser et al. 2020; Walters et al. 2021). Similarly, higher FEve at deeper sites both at the open coast and in the river vicinity (Fig. 4) could be linked to the dominance of deposit-feeding *M. balthica*, known for the ability to switch its dietary habits and feed on suspended OM in favorable conditions (Ólafsson 1986).

Although our model results suggest that deeper sites shared similar functional structures (Fig. 3), the isotopic and functional indices allowed us to capture more subtle differences. For instance, the lack of correlation between IDiv and FDiv (Supporting Information Fig. S6) implies that functions other than those related to foraging might have been responsible for

Table 5. Three-factorial ANOVA of diversity indices: functional and isotopic dispersion (FDis; IDis), evenness (FEve; IEve), and divergence (FDiv; IDiv), and species number (Sp. no.) in the study area ($n = 24$, $df = 1$).

Effect	Sp. no.		FDis		FEve		FDiv		IDis		IEve		IDiv	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Location (Lo)	0.095	ns	2.64	ns	0.21	ns	5.42	*	4.76	*	0.14	ns	0.42	ns
Month (Mo)	0.381	ns	0.44	ns	1.55	ns	1.43	ns	0.06	ns	2.60	ns	0.02	ns
Depth (De)	13.714	**	2.21	ns	16.05	**	0.35	ns	0.84	ns	0.02	ns	0.10	ns
Lo × Mo	0.381	ns	2.03	ns	1.92	ns	0.29	ns	2.01	ns	2.44	ns	0.41	ns
Lo × De	0.381	ns	10.27	**	3.23	ns	2.42	ns	19.39	**	0.04	ns	0.04	ns
Mo × De	0.857	ns	0.38	ns	2.59	ns	0.27	ns	1.09	ns	2.17	ns	0.36	ns

ns, not significant.

* $p < 0.05$;

** $p < 0.01$;

*** $p < 0.00$.

FDiv patterns, such as morphological and behavioral traits. In this meaning, relatively higher FDiv indicates the coexistence of different functional groupings, in which feeding type is only one of many other characteristics deciding about species' ecological roles (Törnroos and Bonsdorff 2012). Therefore, although in Vistula prodelta, FDiv was significantly higher compared to the open coast, this difference could be related to variables other than dietary pool characteristics. Specifically, this could be partially related to significantly higher mud content in the sediments of prodelta that modified functional trait performance, such as greater importance of deep biodiffusers and surface deposit-feeders. Accordingly, when sediment structure was included in the distLM analysis of functional structure (Supporting Information Fig. S5), it occupied the fourth place, explaining an additional 8.06% of the variability ($p = 0.009$, $df = 19$). We, thus, can assume that specific environmental conditions created by the Vistula River plume, such as higher sedimentation and OM supply to the bottom, positively influenced the functional diversity of benthic communities in this area of the Baltic Sea.

Temporal variability

Despite our expectations, we did not find temporal differences between either diversity indices (Table 5) or functional structure (Table 2) of the studied areas. Gogina and Zettler (2023) stated that benthic communities in the southern Baltic Sea reflect rather long-term patterns of productivity in relation to habitat characteristics and food supply. Previous studies in the Vistula prodelta also revealed clear, spatial community patterns resistant to environmental seasonality (Włodarska-Kowalczyk et al. 2016). It could be inferred that although seasonal changes in suspended POM and other environmental characteristics of the water column (salinity, temperature) are strong, they are "typical" for the habitat, and communities have to be accommodated and resistant to such strong changes to persist and maintain vitality and stability of the food web (Bridier et al. 2021). On the other side, the appropriate trophic conditions of the Baltic system and the stability of

the sedimentary pool (this study; Szczepanek et al. 2021), with the main difference being in its quality, may prevent communities from the manifestation of short-time shifts.

Conclusion

In this study, we showed that both functional and isotopic diversity approaches could be effectively combined to get a broader perspective on the relationship between the ecological functions of soft-bottom benthic communities and their food source variability. Functional diversity and structure of benthic communities are most often evaluated using categorical traits since measurements of continuous traits of benthic invertebrates are challenging, and therefore categorical functional characteristics of species are often the only available knowledge (Törnroos and Bonsdorff 2012). Whereas, categorical traits only show the potential niche of species in the community, continuous traits show the fragment of their realized niche space (Törnroos and Bonsdorff 2012; Ehrman et al. 2022). Measuring trophic diversity by stable isotopes provides the assessment of benthic biological traits at a desirable continuous scale (Costello et al. 2015) and enables to include intraspecific variation, which is one of still remaining challenges in functional diversity studies (Petchey and Gaston 2006). Importantly, both approaches allow for including species weighting in the analysis. Assessment of diversity without incorporation of species weighting imposes the assumption, that all species have the same contribution to diversity, which is unrealistic in natural ecological systems (Cucherousset and Villéger 2015).

The specific design of our study enabled us to show that similar assembly mechanisms are important for communities associated with southern Baltic sediments and allowed to distinguish them from the impact of strong environmental filters occurring in this coastal area. Our results confirm previous findings reporting the influence of OM quantity and quality on the functional structure of benthic communities (Dauwe et al. 1998; Hudson et al. 2003; Wieking and Kröncke 2005)

and allow to conclude that greater variability in food supply generates higher functional diversity of benthic communities.

Data availability statement

The raw data supporting the conclusions of this article will be made available on request from the authors.

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Acknowledgments

The authors would like to acknowledge the Captain and the Crew of s/y Oceania for their help in acquiring marine samples. We thank Dr. Aleksandra Winogradow, Dr. Katarzyna Koziorowska-Makuch, Zuzanna Borawska, Patrycja Nowakowska, and Michał Gintowt for their help in collecting and analyzing chemical and biological samples. We are also grateful to all the students who helped with macrofauna sorting and identification. The study was funded by the Polish National Science Centre project no. 2020/37/N/NZ8/01418 (ISOFUN) granted to M. Szczepanek and, additionally, project no. 2017/26/E/NZ8/00496 (COMBACK) granted to M. Kedra. The original research in this publication first appeared in the first author's PhD thesis (Szczepanek 2023).

Conflict of Interest

None declared.

Submitted 10 May 2023

Revised 11 August 2023

Accepted 22 December 2023

Associate editor: Anna R. Armitage