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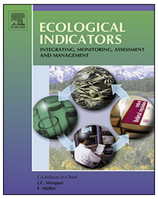

Functional trait composition and diversity patterns of marine macrobenthos across the Arctic Bering Sea

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ABSTRACT

The use of functional trait analysis has been advocated to uncover the global mechanisms behind biodiversity responses to environmental variation, but the application of this approach to the Arctic macrobenthic community is underdeveloped relative to that used for other organism groups. Based on several summer surveys (July to September 2010, 2012, 2014 and 2016) in the Bering Sea, we used biological trait analysis (BTA) to quantify the composition and diversity of macrobenthic biological traits along an environmental gradient ranging from the shallowest portion of the continental shelf to the shelf break and deep basin. Our results show a clear shift in the macrobenthic functional composition through the application of abundance- and biomass-based measurements in six different subregions of the Bering Sea. The macrobenthic community of the south-western shelf and shelf break of the Bering Sea, an area with silty-sand sediment, was mainly composed of taxa characterized by high body flexibility, vermiform, and tube-dweller/burrower modalities or large, semi-motile, deposit feeder and flattened dorsally modalities. However, the community of the north-eastern shelf of the Bering Sea with sandy sediment was mainly characterized by organisms characterized as motile surface crawlers and carnivores/scavengers. Similar to the factors that determine the taxonomic distribution and composition of the macrobenthos, sediment composition and depth were found to be the main factors that affect the distribution of the macrobenthic functional structure in the study area. The species and functional diversity of the macrobenthos show a strong linear relationship, potentially indicating that the community exhibits relatively low functional redundancy and that the benthic ecosystem is vulnerable to species loss or regime shifts.

1. Introduction

The Bering Sea is the only link between the Arctic Ocean and the Pacific Ocean; nutrient-rich Pacific waters pass through the Bering Sea Strait and Chukchi Sea to flow into the Arctic Ocean (Woodgate and Aagaard, 2005; Hunt et al., 2013). The hydrological conditions of the Bering Sea are relatively complicated (Fig. 1) and are mainly influenced by Anadyr Water, Alaska Coastal Water and Bering Shelf Water (Weingartner et al., 2005). Despite being located at a high latitude and experiencing 7–8 months of seasonal ice cover, the Bering Sea remains one of the world's most productive regions (Grebmeier et al., 1989; Lin et al., 2018). The diverse currents and high primary productivity in the Bering Sea provide favourable conditions for the growth and reproduction of macrobenthos (Lin et al., 2016).

The macrobenthos in marine systems plays important roles in nutrient cycling, sediment oxygenation, and organic matter decomposition (Constable, 1999; Bremner, 2005). Many ecologists have described the macrobenthic community structure and secondary production of the Bering Sea, and sought to relate species patterns and dynamics to environmental conditions and external factors (Grebmeier et al., 2006; Wang et al., 2014; Lin et al., 2018). Climate change and sea ice retreat have been clearly concluded to be the main factors affecting Arctic marine species, taxon groups and local assemblies. However, an understanding of how certain ecosystem processes work is considerably lacking, let alone how overall ecosystem functioning will be affected (Degen et al., 2018). The key reason for this uncertainty is that we lack

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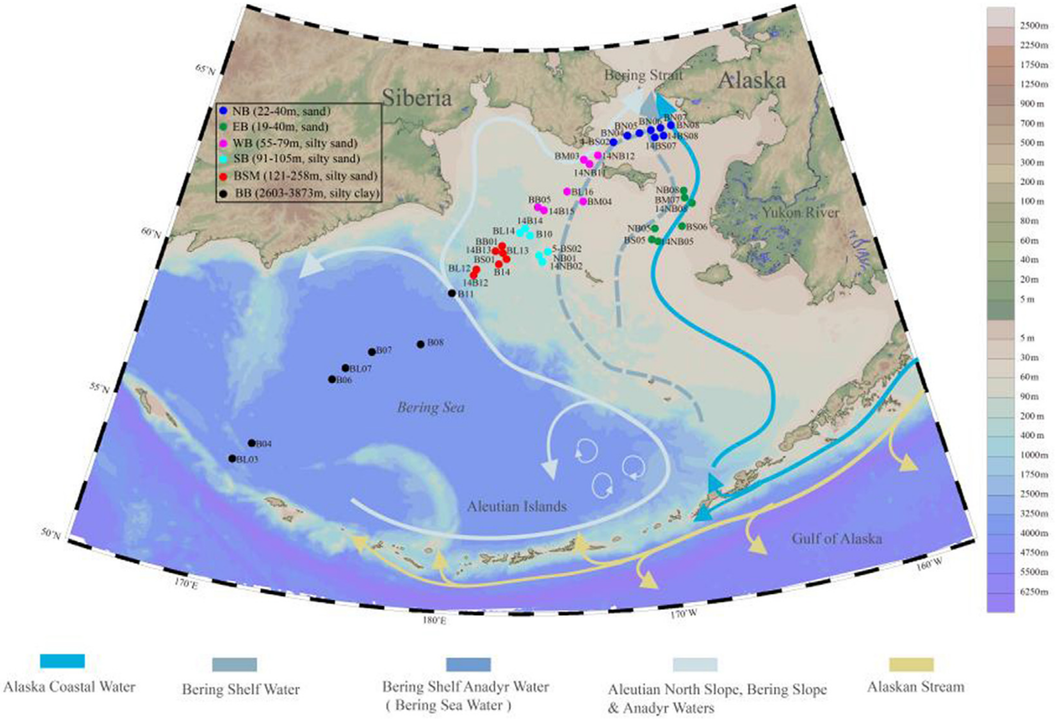

Fig. 1. The Bering Sea and the sampling locations.

knowledge of community structure-function relationships (Worm et al., 2006). Functional characteristics are known to strongly influence ecosystem properties and, as such, provide an important link between taxonomic community structure and ecosystem functioning (Wong and Dowd, 2015).

Functional characteristics or 'traits' are the morphological, physiological, phenological or behavioural features of an organism that describe its performance (Violle et al., 2014), including the interactions of organisms with one another and with their physical and chemical environments (Bremner et al., 2006a). Traits are often used as surrogates for ecosystem properties because the composition and structure of these traits have been demonstrated to affect multiple ecosystem functions, such as nutrient cycling, primary and secondary production, and sediment erodibility (Norkko et al., 2013; Bolam and Eggleton, 2014). Therefore, trait-based approaches, together with traditional taxonomic methods, have become useful tools in ecosystem monitoring and management (Tomanova et al., 2008; Rand et al., 2018).

Biological trait analysis (BTA) is a technique that uses a series of life history, morphological and behavioural characteristics of the species present in assemblages to understand the structures and dynamics of ecological communities (Bremner et al., 2006a). BTA combines structural data for species assemblages with information on the functional features of each species, which can then be used for analyses of their relationships with environmental factors, providing information on the connections among species, the environment and ecosystem processes (Bremner, 2005). This approach has been used most recently in other Arctic macrobenthic communities, including those in the Barents Sea, Chukchi Sea, Laptev Sea and Canadian Arctic (Cochrane et al., 2012; Rand et al., 2018; Kokarev et al., 2017; Krumhansl et al., 2016). The Bering Sea, as one of several extraordinarily productive subarctic seas, lacks studies on the functional structure of macrobenthic communities under various environmental factors using the BTA approach. In addition, previous studies in the Arctic used either abundance, biomass or other data for weighing functional traits, but no study has compared the effects of different weighted values on the result of macrobenthic functional structure.

In this paper, we use BTA for the first time to compare and contrast the taxonomic and functional composition and diversity of macrobenthic communities in the Bering Sea. The data mainly come from the 4th, 5th, 6th and 7th Chinese National Arctic Research Expeditions (CHINAREs). The survey area extends from the northeast continental shelf to the deep basin in the southwest, presenting visible gradients in depth. In brief, our aim is to (1) compare the functional composition and diversity of macrobenthos based on abundance and biomass, (2) analyze the relationship between taxonomic and functional diversity and (3) explore the biological traits of the macrobenthic communities in response to the high variability of environmental gradients. This study will contribute to a better understanding of the ecological functioning of macrobenthic communities in Arctic marine ecosystems in the context of global climate change.

2. Materials and methods

2.1. Study area

The Bering Sea, a northern extension of the Pacific Ocean, separates the continents of Asia and North America. The sea is bordered to the west by Russia and the Kamchatka Peninsula, to the south by the Aleutian Islands, and to the east by Alaska. The Bering Sea is a highly heterogeneous system, with water depths ranging from approximately 20 m along the shallow continental shelf in the northeast to approximately 4000 m in the deep depressions in the south. Bottom sediments range from gravel and sand, to fine silt. The key water mass types of this region are defined primarily by seasonally varying salinity in the spring and summer. The main currents here are the more saline, nutrient-rich Anadyr Water (salinity > 32.5), which moves northward from the western side, the fresher, more nutrient-limited Alaska Coastal Water (salinity < 31.8), which flows northward from the eastern side, and the nutrient-rich Bering Shelf Water, which has intermediate salinity ($31.8 < \text{salinity} < 32.5$) and lies between the Anadyr Water and Alaska Coastal Water (Grebmeier et al., 2006). The high-nutrient Bering Shelf Water offshore water and the low-nutrient Alaska Coastal Water form a strong frontal system that has an important influence on the primary productivity in this region (Grebmeier et al., 1988). As these

Table 1
Biological trait variables and modalities in the macrobenthic assemblages of the Bering Sea.

Biological traits	Trait modalities	Trait code	Ecosystem functions and properties
Morphology			
Normal adult size	Small (< 1cm)	S1	Metabolic rate varies with body size, influencing all activities of organisms and subsequently all ecosystem functions of interest here (Brown et al., 2004).
	Small-medium (1–6 cm)	S2	
	Medium-large (6–10 cm)	S3	
	Large (> 10 cm)	S4	
Body form	Globulose	BF1	The trait influences movement ability through sediments and ability to move sediments (Norling et al., 2007).
	Vermiform	BF2	
	Flattened dorsally	BF3	
	Flattened laterally	BF4	
	Upright	BF5	
	Conical	BF6	
Body flexibility (degrees)	High (> 45)	FL1	The trait reflects the ability of organisms to respond to environmental changes (Tomanova et al., 2008).
	Low (10–45)	FL2	
	None (< 10)	FL3	
Life history			
Longevity (years)	Short (≤2)	A1	The crucial ecological trait can reveal the resilience of an organism in the presence of a disturbance (de Juan et al., 2007).
	Medium (2–5)	A2	
	Long (> 5)	A3	
Larval development	Planctonic	LD1	The trait reflects the ability of organisms to spread over temporal and spatial scale and influences nutrient cycling (Degen et al., 2018).
	Benthic	LD2	
Behavior			
Living habit	Attached	LH1	The trait creates habitat complexity and can influence production and trophic support (Callaway, 2006).
	Tube-dweller	LH2	
	Burrower	LH3	
	Surface crawler/ Swimmer	LH4	
Mobility	Sessile	Mob1	The trait is crucial for macrobenthos not only regarding the avoidance of physical disturbance but also in the predatory-prey activities or the construction of biological structures (Hinchey et al., 2006).
	Semi-motile	Mob2	
	Motile	Mob3	
Degree of attachment	None	DA1	The trait influences metabolic requirements and thus production and trophic support (Brown et al., 2004).
	Temporary	DA2	
	Permanent	DA3	
Feeding habit	Suspension/filter feeder	FH1	The central factor of macrobenthos communities construction; all feeding types contribute to production and trophic support, and nutrient cycling (Norling et al., 2007).
	Scraper/grazer	FH2	
	Deposit feeder	FH3	
	Scavenger	FH4	
	Carnivore/omnivore	FH5	
Position in sediment	Infauna	EP1	The position occupied in sediment influences surface mixing, sediment transport and burial, nutrient cycling, and sediment oxygenation (Wong and Dowd, 2015).
	Epifauna	EP2	
Bioturbation	Surface mixing	B1	Sediment transport from redistribution and mixing of particles influences the carbon sequestration, sediment oxygenation, and nutrient cycling (Mermillod-Blondin et al., 2004).
	Deeper mixing	B2	
	Transport	B3	
	None	B4	

waters flow north through the Bering Strait, the Anadyr Water and Bering Shelf Water mix to form a modification of the Bering Shelf Water referred to as the Bering Shelf-Anadyr Water. The melting of sea ice in the Bering Sea shows obvious seasonality. In winter, 75% of the northern continental shelf is covered, and the ice thickness is between 1 and 2 m, whereas the entire sea area is free of ice in summer.

The sampling stations are strategically located at various depths, salinities, sediment types and organic matter contents, including the continental shelf, shelf break and deep basin. Affected by Alaska Coastal Water and the Yukon and Kuskokwim rivers, the salinity of the eastern Bering Shelf is relatively low; a large number of coarse-grained terrigenous compositions enter the area along the rivers, resulting in sand-dominated sediments in the area. The northern shelf is affected by the strong currents at the Bering Strait, fine sediments are removed, and relatively coarse components are left behind. Due to the existence of the main currents, such as the Bering Shelf Water, Anadyr Water and Bering Shelf-Anadyr Water in the southwest shelf and continental slope area, the surface sediments are somewhat sorted, which mean the area is dominated by silty sand. The silt and clay contents are higher from the northwest Aleutian Basin to the island slopes of the Aleutian Islands of the Bering Sea (Chunjuan et al., 2015; Smith and McConnaughey, 1999). Fig. 1 shows the sampling stations relative to the position of the surface currents in the Bering Sea.

2.2. Data collection

2.2.1. Biological data

Macrobenthic samples were collected at 42 stations in the Bering Sea (Fig. 1) from aboard the R/V Xuelong during the 4th (July to September 2010), 5th (July to September 2012), 6th (July to September 2014) and 7th CHINAREs (July to September 2016). Water depth is known to be the driving parameter of changes in the macrobenthic community structure (Darr et al., 2014). Therefore, six distinct subregions were defined based on the depth gradient, which runs from the shallowest continental shelf through the shelf break to the deep basin, including the northern Bering Shelf (NB, 8 stations at depths ranging from 22 m to 40 m), the eastern Bering Shelf (EB, 7 stations, 19 m to 40 m), the western Bering Shelf (WB, 7 stations, 55 m to 79 m), the southern Bering Shelf (SB, 6 stations, 91 m to 105 m), the Bering shelf break (BSM, 7 stations, 121 m to 258 m), and the Bering basin (BB, 7 stations, 2603 m to 3873 m).

One sediment sample per station was collected using a 0.25 m^2 box corer (50 cm*50 cm*60 cm). Each sample was sifted through mesh with a pore size of 0.5 mm to collect the macrobenthic organisms, which were fixed in a 7% formaldehyde solution and transported to the laboratory for species identification, counting, and weighing (fresh mass). Ash-free dry mass (afdm) was calculated from the fresh mass using conversion factors based on Brey (2001). For colonial animals, such as sponges, the counts were based on a single individual (Griffiths et al., 2008). Taxon names were cross-checked against the World Register of Marine Species (http://marinespecies.org/). Finally, the taxa abundance and biomass (afdm) data from each station were used to construct numerical matrices ('taxa by stations' matrices).

2.2.2. *Environmental data*

During the collection of sediment samples, the bottom salinity was quantified at each station using a Sea-Bird Electronics (SBE911 Plus) conductivity-temperature-depth (CTD) system. In the laboratory, grain composition analysis (percentages of sand, silt and clay) of the filtered subsamples was performed for each station using a Malvern Mastersizer Laser Particle Size Analyzer according to Yao et al. (2014). Median particle diameter (Md) and sorting values were also calculated. The total organic carbon (TOC) and total nitrogen (TN) contents in the sediments were measured with a CHN analyser (Vario EL III) after the samples were freeze-dried according to Qiao et al. (2011).

2.3. *Data matrices*

Eleven biological traits subdivided into 42 modalities were used to describe the important functional attributes of the macrobenthic community in the Bering Sea. The traits chosen were those known to influence ecosystem functions (e.g., nutrient cycling, sediment transport, production and trophic support) (Wong and Dowd, 2015) and included morphological (normal adult size, body form and body flexibility), behaviour (living habit, mobility, degree of attachment, feeding habit, position in the sediment and bioturbation), and life history (longevity and larval development) characteristics, and most of them have already been used in other BTA studies in the Arctic (Degen et al., 2018). Functional traits used in the study and their connection to ecosystem functions relevant to the macrobenthos are provided in Table 1.

A fuzzy coding approach was used to classify each species according to its association with the different modalities of the functional traits (Chevenet et al., 1994). Each trait modality was assigned a value of 0, 1, 2, or 3 for each species, where no affinity was coded as 0 and complete affinity was coded as 3. In this study, to avoid bias among the different modalities, the affinity scores for each trait were standardized so that the sum was equal to 1 (Darr et al., 2014). For example, the polychaete *Eteone foliosa*, as a carnivore as well as a scavenger, prefers to eat live animals; therefore, the affinity scores were '3' and '1' for 'Carnivore' and 'Scavenger', respectively, equaling '0.75 and 0.25' after standardization (Chevenet et al., 1994). Information regarding the functional traits of each species was gathered from the literature (Degen, 2015; Kokarev et al., 2017; Darr et al., 2014; Bremner, 2005) and various online sites and databases (WoRMS Editorial Board, 2018; Polytraits Team, 2018; MarLIN, 2006; Degen and Faulwetter, 2018). When little or no information on a species' life history could be found, information from other species within the same genus or family was used (Rand et al., 2018).

Next, three matrices were constructed for the analysis: (1) macrobenthic abundance or biomass (afdm) at each station (L table: 'taxa abundance or biomass by samples' matrix), (2) biological traits of each species (Q table: 'taxa by traits' matrix), and (3) the combination of the previous two biological traits at each station (LQ table: 'traits by stations' matrix). In this study, abundance and biomass (afdm) were both chosen as response variables for the linkage of the L table to the Q table in independent analyses. Before the analysis, taxa abundance and biomass (afdm) data were transformed by ln (1 + x) to reduce the bias caused by dominant species.

2.4. *Taxonomic and functional diversity*

To obtain an impression of the characteristics of the macrobenthic communities within the different subregions in the Bering Sea, the four most frequently used taxonomic diversity indexes, richness (number of species), abundance, biomass and Shannon-Wiener diversity (H′, logarithm based on log2), were calculated. Functional diversity (FD) was estimated by Rao's quadratic entropy (RQE), which is commonly used to calculate FD because it takes functional richness, functional evenness and functional divergence into account (Van Der Linden et al., 2012). We used the functional redundancy index, calculated as the ratio of FD to species diversity (FD/H′), to assess the relationship between taxonomic and functional diversity. An increase in the ratio indicates a decrease in functional redundancy and *vice versa* (Van Der Linden et al., 2012). Differences in the values of the indexes mentioned above among the different subregions were tested with the non-parametric Kruskal–Wallis (KW) test (Kruskal and Wallis, 1952). We also examined the relationships between species and functional diversity at each station using a linear regression model. The four root transformation was performed before the analysis.

2.5. *Statistical analysis*

Variation in the environmental factors among the different subregions in the Bering Sea was analysed using principal component analysis (PCA). To eliminate the effects of data dimensions (units), the environmental variables were transformed by ln (1 + x).

A major development in BTA was provided by Chevenet et al. (1994) through fuzzy correspondence analysis (FCA). FCA is derived from the correspondence analysis (CA) ordination method and is appropriate for use with fuzzy coded data (Chevenet et al., 1994). In this study, based on the 'traits by stations' matrix (LQ table), we used FCA to identify the differences in functional composition among the different subregions in the Bering Sea. To identify the traits that were most responsible for the variation along the principal factorial axes for all subregions, FCA was conducted for the two different versions of the 'traits by stations' matrix, once for the abundance matrix and once for the biomass (afdm) matrix.

Statistical analysis was performed with R-3.4.4 open-source software with the packages ade4 (Dray and Dafour, 2007) and vegan (Oksanen et al., 2018). All diversity indexes were calculated with the FDiversity software (Casanoves et al., 2011).

3. Results

3.1. *Environmental conditions*

The average values of the environmental variables for each

Table 2
Mean values (± SD) of environmental variables in the different subregions of the Bering Sea.

	Depth	Md	sand%	silt%	clay%	TOC	TN	bottom salinity	Sediment type
EB	32 ± 6	3.26 ± 0.43	74.8 ± 10.1	22.2 ± 8.8	3.0 ± 1.2	0.31 ± 0.13	0.06 ± 0.02	31.54 ± 0.59	Sand
NB	34 ± 6	2.21 ± 0.49	90.2 ± 7.8	8.2 ± 6.4	1.6 ± 1.4	0.20 ± 0.08	0.06 ± 0.01	32.42 ± 0.36	Sand
WB	64 ± 11	4.55 ± 1.67	37.3 ± 30.6	52.2 ± 25.6	10.6 ± 5.3	0.94 ± 0.59	0.15 ± 0.08	32.42 ± 0.32	Silty sand
SB	97 ± 5	5.86 ± 0.4	15.5 ± 12.4	71.8 ± 11	12.7 ± 4.2	1.62 ± 0.22	0.22 ± 0.02	32.30 ± 0.2	Silty sand
BSM	159 ± 52	4.69 ± 0.84	40.5 ± 18.8	50.3 ± 14.8	9.2 ± 4.4	1.27 ± 0.52	0.14 ± 0.06	32.95 ± 0.3	Silty sand
BB	3578 ± 405	6.66 ± 0.7	8.2 ± 8.7	67.9 ± 4.9	23.9 ± 8.9	1.12 ± 0.55	0.17 ± 0.06	34.65 ± 0.02	Silty clay

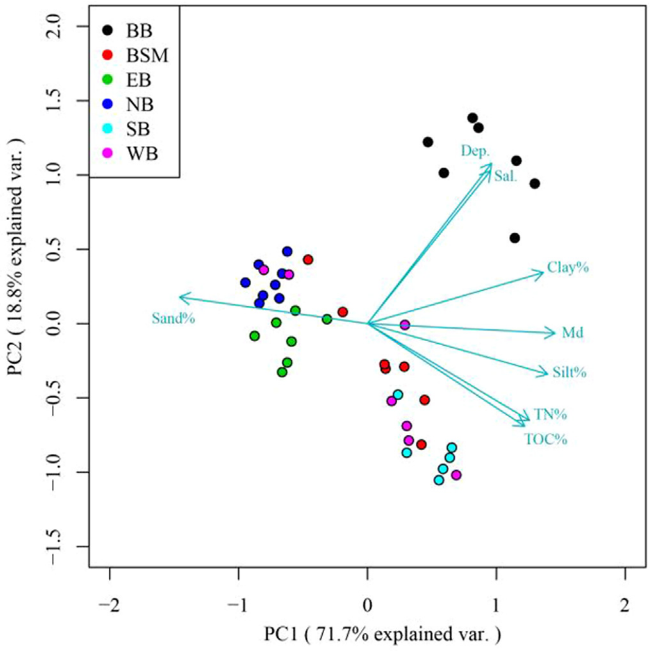

Fig. 2. Principal component analysis of the relevant environmental variables in the Bering Sea.

subregion are displayed in Table 2. The PCA ordination of the 8 environmental variables revealed gradients along the first two axes (Fig. 2). The first axis explained 71.7% of the total variability and was associated with changes in the sediment particle size (Md, sand%, silt%, and clay%) and organic matter (TOC and TN). The EB and NB subregions differed from the other subregions of the Bering Sea, as they had a higher percentage of sand. The WB (except 14NB11 and 14NB12), BSM (except BL12 and 14B12) and SB subregions of the Bering Sea were characterized by a higher Md and greater percentages of silt and clay and contents of TOC and TN. The second axis explained 18.8% of the total variability and was associated with changes in depth and bottom salinity. The BB subregion had the greatest depth and bottom salinity (Table 2), while the continental shelf is relatively shallow, and the bottom salinity is therefore easily affected by inputs from rivers, precipitation and melting ice.

3.2. Taxonomic composition of the macrobenthic community

A total of 232 different taxa were identified in the study area, of which polychaetes were the most abundant, with a total of 114 species, whereas there were 42, 43 and 10 crustacean, mollusc and echinoderm species, respectively. Among the six subregions, the SB had the highest species richness (17 species, Fig. 3c), NB had the highest abundance (1651 ind/m^2, Fig. 3a), and WB had the highest biomass (afdm) (119.0 g afdm/m^2, Fig. 3b). Meanwhile, species diversity (Shannon-Wiener diversity) was the lowest in the BB ($H' = 0.62$) and highest in the SB ($H' = 2.65$) (Fig. 3d).

The macrobenthic abundance, biomass (afdm), species richness and species diversity of the BB showed significantly lower values compared to those of other subregions ($p < 0.01$ for all pairwise comparisons in the KW test). No significant differences in these parameters were found among the EB, NB, WB, SB and BSM ($p > 0.05$ for all pairwise comparisons in the KW test).

The composition of the dominant taxa differed among the subregions in the study area (Table 3). The polychaetes *Scoloplos (Scoloplos) armiger* and *Tharyx* sp. and crustaceans *Maera danae* and *Eudorella pacifica* were the most abundant species, with each of these species accounting for more than 10% of the overall abundance in each subregion. The species with the second highest abundances in the EB and BSM were the bivalve *Ennucula tenuis* (12.2%) and ophiuroid *Ophiura sarsii* (12.9%), respectively. Based on biomass (afdm), the asteroid *Ctenodiscus crispatus* was the dominant species in both the SB (18.1%) and BSM (38.9%). The echinoid *Echinarachnius parma* and cnidarian Zoanthidae und. dominated the biomass in the NB and WB, respectively, reaching comparably high values (more than 50% of the overall biomass). The crustacean *Pagurus pubescens* and polychaete *Nephtys caeca* exhibited higher biomass in the EB, with percentages of 23.1% and 11.8%, respectively.

3.3. Biological trait analysis

Two separate FCAs based on abundance and biomass (afdm) were performed to analyse the functional composition of the macrobenthic community in the Bering Sea.

The FCA based on abundance accounted for 44.1% of the total variance in the distribution of traits for the Bering Sea, with 25.8% explained by axis 1 and 18.3% by axis 2 (Fig. 4). The contribution of each trait to this overall variability was reflected in the correlation ratios (Table 4). Correlation ratios greater than 10% ($RS > 0.1$) can be considered as the traits with the most variable distribution (Conti et al., 2014). The biological traits separated along axis 1 were dominated by mobility, feeding habit and living habit, whereas those separated along axis 2 were dominated by adult size. Body form and flexibility were strongly correlated with both axes. The ordination plots for all traits and their modalities are shown in Fig. 5.

The NB and BB subregions were located on the positive side of axis 1, corresponding to preferences for low body flexibility, motile, carnivore/scavenger and surface crawler modalities. The WB, SB and BSM subregions were located on the negative side of axis 1, with macrobenthos assemblages dominated by species that are flattened dorsally/upright, sessile/semi-motile, deposit feeders and tube-dwellers/burrowers (Figs. 4 and 5). Such assemblages were found in association with rich nutrients and higher percentages of silt and clay (Figs. 2 and 4). The WB, NB and EB subregions, with positive axis 2 scores, were dominated by assemblages composed of species that are flattened laterally/upright/conical and small/small-medium in size. The SB, BSM and BB subregions had negative axis 2 scores and were characterized by high body flexibility, medium-large/large and vermiform modalities (Figs. 4 and 5).

The FCA based on biomass (afdm) accounted for 39.5% of the total variance in the distribution of traits, of which 21.9% was explained by axis 1 and 17.6% was explained by axis 2 (Fig. 6). The biological traits separated along axis 1 were dominated by longevity and position in the sediment, whereas those separated along axis 2 were dominated by mobility, degree of attachment and body flexibility. Living habits, body form and bioturbation were strongly correlated with both axes.

The modalities of attached, globose/upright, epifauna, long longevity and no bioturbation were separated along the right side of axis 1, as was the WB subregion (Figs. 6 and 7). The NB, EB and BB subregions were concentrated on the left side of axis 1 and were dominated by the tube-dweller, vermiform/flattened laterally, infauna, short longevity and deeper mixing/transport modalities. The upper part of axis 2 corresponded to the modalities of temporary/permanent, sessile/semi-motile and high body flexibility, and this macrobenthos assemblage was found in sediments with higher percentages of silt and clay and rich nutrients (WB, SB and BSM). The NB and EB subregions occurred on the lower part of axis 2, with significant contributions of the surface crawler, no attachment, motile, flattened dorsally/conical, low/no body flexibility and surface mixing modalities (Figs. 6 and 7).

The separations of the trait modalities along the first two axes and also their correlations based on both species abundance and biomass (afdm) were strong in the study. The ordination of the traits by stations showed an overlap of the investigated areas, but the subregions with gradients of different water depths and sediment particle size were

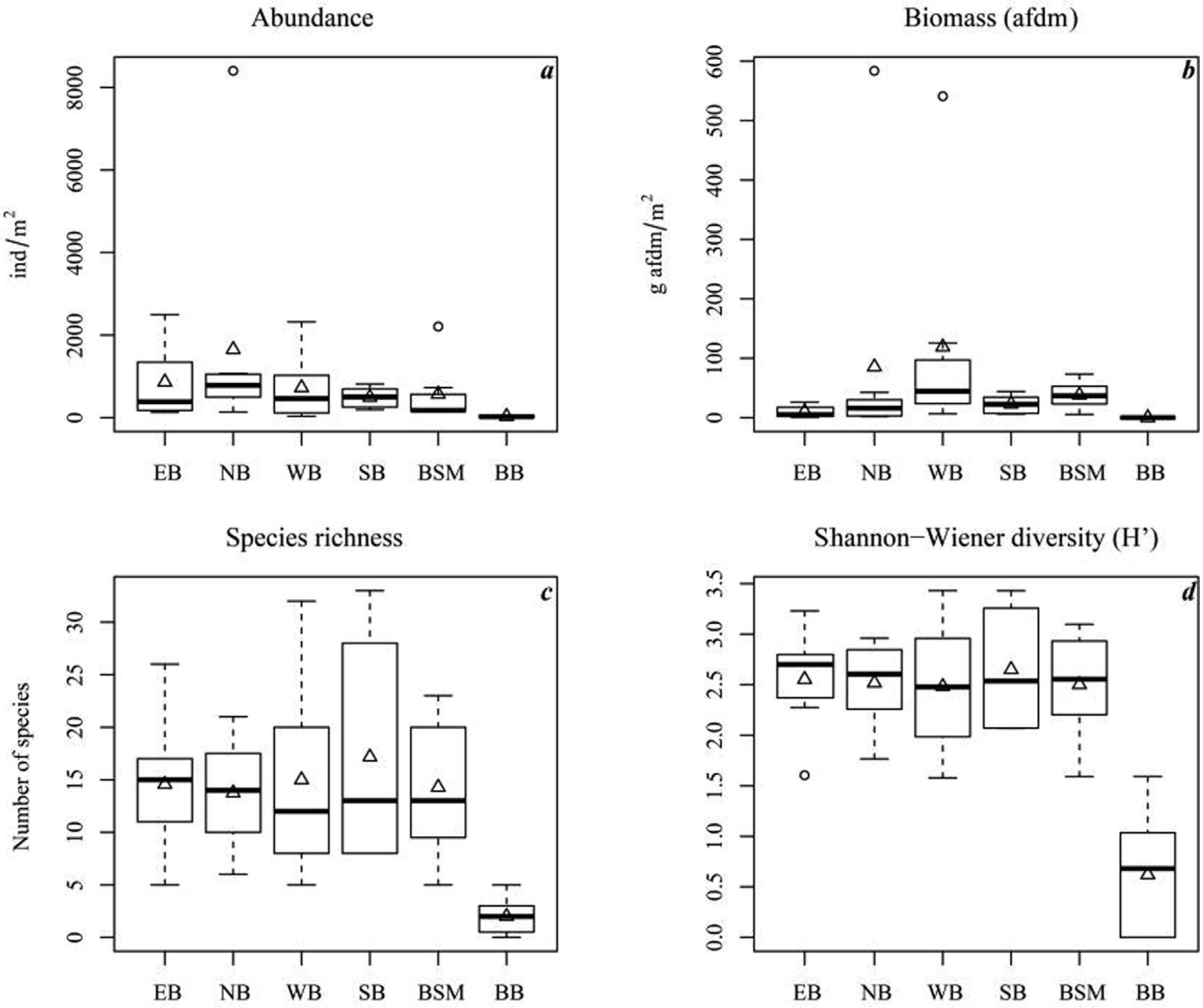

Fig. 3. Boxplots of the abundance, biomass (afdm), species richness and diversity in the six subregions. The small triangles and open circles represent the average values and outliers, respectively.

mostly separated. Mobility, feeding habit and living habit were the most relevant traits based on abundance in distributing the stations along axis 1. Longevity and position in the sediment were the most relevant traits based on biomass in distributing the stations along axis 1.

3.4. Functional diversity and functional redundancy

There were no significant differences in FD based on the transformed abundance and biomass (afdm) among the six subregions ($p = 0.075$ and $p = 0.078$ in the KW test, respectively; Fig. 8a and b). The FD based on abundance was slightly higher in the WB (4.85 ± 0.54) than that in the other continental shelf and slope subregions, and the SB (4.77 ± 0.57) showed the highest FD values based on biomass. The BB had the lowest FD values based on both abundance and biomass (Fig. 8a and b).

The highest functional redundancy based on abundance and biomass (afdm) were both found in the EB (FD/H′ values were 1.79 ± 0.27 and 1.42 ± 0.32, respectively), and the lowest values occurred in the WB (FD/H′ value based on abundance was 2.07 ± 0.46) and BB (FD/H′ value based on biomass was 1.96 ± 0.78) (Fig. 8c and d). There was a significant positive relationship between species and functional diversity (based on abundance: $F = 392.9$, d.f. = 38, $p < 0.001$, linear $R^2 = 0.910$, slope = 1.11; based on biomass (afdm): $F = 211.3$, d.f. = 38, $p < 0.001$, linear $R^2 = 0.844$, slope = 1.09) (Fig. 9).

4. Discussion

4.1. Selection of traits and weighted values

The interpretation of the BTA depends upon the traits selected during the analytical process (Bremner et al., 2006b; Lefcheck et al., 2015). Different traits can show distinct variation in the trends of their modalities along environmental gradients (Lavorel and Garnier, 2002). Costello et al. (2015) reviews the utility and availability of biological traits for marine species and considers that 10 traits, including taxonomic classification, environment, geography, depth, substratum, mobility, skeleton, diet, body size and reproduction, should be preferentially used in studies. However, finding literature information regarding the traits of numerous species is difficult and time-consuming; gaps in knowledge of species biology make it impossible to complete the coding of some traits for all species (Munari, 2013), particularly at high latitudes. In this study we focused on biological traits related to morphology, behaviour and life history that we could most easily code, without having to use 0 for all modalities, including 11 biological traits subdivided into 42 modalities. The selected traits and modalities were those that were most widely used in benthic invertebrate trait studies published from 1979 to 2018 (Degen et al., 2018) and maximize some of the fundamental differences in the biology and ecology of species (Rand et al., 2018).

All of the traits used in this study, except for 'Larval development'

Table 3
The top five most dominant taxa in terms of abundance (left) and biomass (right) are listed for the subregions of the Bering Sea to characterize their macrobenthic communities.

Taxa	Abundance (ind/m^2)	Percentage	Taxa	Biomass (g afdm/m^2)	Percentage
EB					
Scoloplos armiger	199	23.1%	*Pagurus pubescens*	2.3	23.1%
Ennucula tenuis	105	12.2%	*Nephtys caeca*	1.2	11.8%
Byblis gaimardii	59	6.9%	*Scoloplos (Scoloplos) armiger*	0.9	9.1%
Harpiniopsis vadiculus	32	3.7%	*Nephtys ciliata*	0.8	8.3%
Glycinde wireni	30	3.5%	*Yoldia amygdalea*	0.6	5.9%
NB					
Maera danae	497	30.1%	*Echinarachnius parma*	55.7	65.2%
Eudorella pacifica	129	7.8%	*Chionoecetes opilio*	17.3	20.3%
Scoloplos (Scoloplos) armiger	115	7.0%	*Nicolea* sp.	2.3	2.7%
Maldanidae und.	97	5.9%	*Nephtys caeca*	1.7	2.0%
Leptochelia dubia	75	4.5%	*Bugula* sp.	1.4	1.7%
WB					
Scoloplos armiger	95	13.1%	Zoanthidae und.	68.4	57.5%
Leitoscoloplos pugettensis	58	7.9%	*Golfingia margaritacea*	8.7	7.3%
Macoma calcarea	45	6.2%	*Nephtys* sp.	5.6	4.7%
Pontoporeia femorata	42	5.8%	*Gersemia rubiformis*	5.3	4.4%
Lumbrineris sp.2	40	5.5%	*Modiolus modiolus*	4.0	3.4%
SB					
Tharyx sp.	51	10.3%	*Ctenodiscus crispatus*	4.1	18.1%
Leitoscoloplos pugettensis	48	9.7%	*Axiothella catenata*	3.8	16.5%
Ophiura sarsii	44	9.0%	*Axiothella rubrocincta*	2.4	10.8%
Lumbrineris sp.	24	4.9%	*Haliplanellidae* sp.	1.9	8.6%
Heteromastus filiformis	24	4.8%	*Serripes laperousii*	1.9	8.5%
BSM					
Eudorella pacifica	91	15.9%	*Ctenodiscus crispatus*	14.8	38.9%
Ophiura sarsii	74	12.9%	*Maldane sarsi*	3.7	9.7%
Scoletoma fragilis	50	8.7%	*Virgularia* sp.	3.3	8.6%
Heteromastus filiformis	32	5.6%	*Megayoldia thraciaeformis*	2.1	5.5%
Harpiniopsis vadiculus	30	5.2%	*Ophiura sarsii*	1.8	4.8%
BB					
Polynoidae und.	7	23.1%	Polynoidae und.	0.0099	18.9%
Dasybranchethus fauveli	2	7.7%	Nemertea und.3	0.0096	18.4%
Pilargis verrucosa	2	7.7%	*Prionospio malmgreni*	0.0066	12.6%
Prionospio malmgreni	2	7.7%	*Ampelisca brevicornis*	0.0037	7.0%
Ampelisca brevicornis	2	7.7%	*Corophium* sp.	0.0037	7.0%

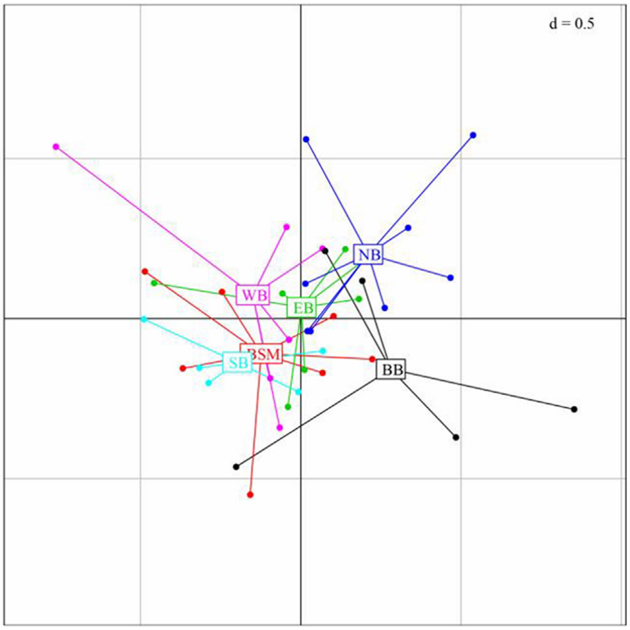

Fig. 4. Two-dimensional FCA plots weighted by abundance showing the distribution of the different subregions.

Table 4
Correlation ratios (RS) of the first two axes of the FCA. Bold figures indicate traits with the most variable distribution.

	Based on abundance		Based on biomass (afdm)	
Trait	RS1	RS2	RS1	RS2
Living habit	**0.120**	0.019	**0.258**	**0.223**
Degree of attachment	0.044	0.012	0.051	**0.151**
Mobility	**0.160**	0.001	0.018	**0.214**
Body form	**0.163**	**0.243**	**0.389**	**0.211**
Body flexibility	**0.161**	**0.142**	0.039	**0.129**
Normal adult size	0.044	**0.104**	0.062	0.004
Feeding habit	**0.123**	0.073	0.097	0.089
Position in the sediment	0.045	0.000	**0.134**	0.076
Longevity	0.095	0.048	**0.221**	0.019
Larval development	0.021	0.001	0.093	0.045
Bioturbation	0.025	0.068	**0.281**	**0.160**
Variance	25.80%	18.30%	21.9%	17.6%
Eigenvalues	0.091	0.065	0.149	0.120

($RS < 0.1$ in both approaches), were found to be useful for describing the observed patterns and significantly contributed to the first two axes in the FCA. Similar results were also reported by Paganelli et al. (2012). Larval development, as a response trait, can reflect macrobenthos juvenile survival and dispersal potential (Beauchard et al., 2017) and is especially important in terms of the analysis of colonization and recolonization after disturbance (Boström et al., 2010; Pacheco et al., 2013). However, this trait is not closely relevant to sediment-related

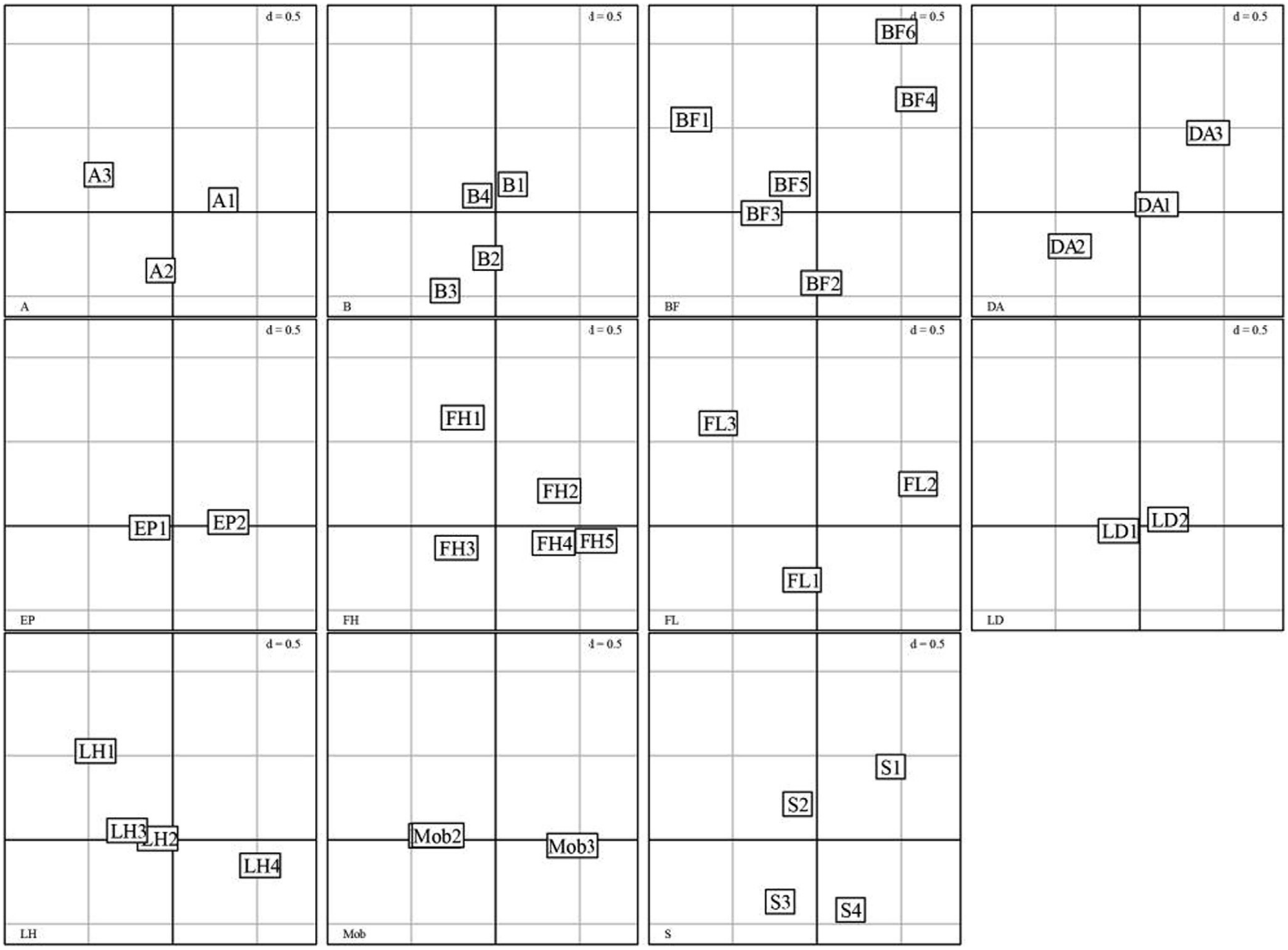

Fig. 5. Two-dimensional FCA plots weighted by abundance showing the distribution of the trait modalities. See Table 1 for labels.

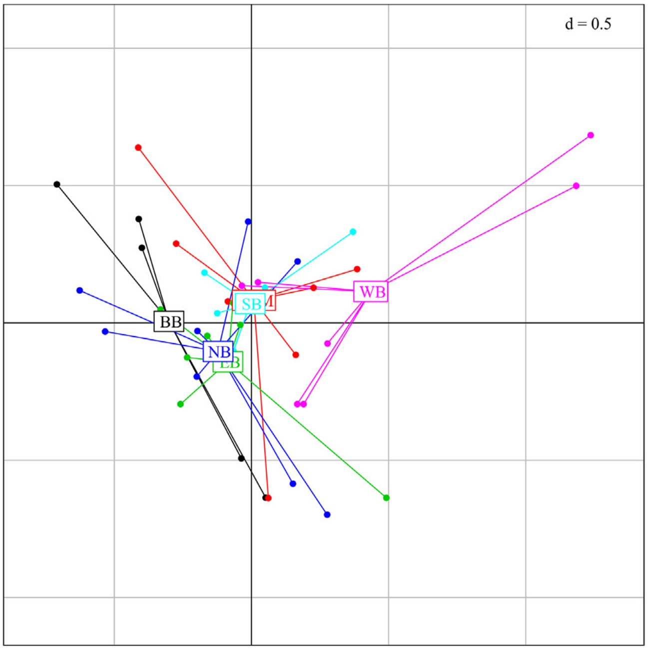

Fig. 6. Two-dimensional FCA plot weighted by biomass (afdm) showing the distribution of the different subregions.

processes in the Bering Sea. Furthermore, the life history information on macrobenthos is largely absent for high latitudes. The Arctic Traits Database is a trait platform for Arctic benthos (Degen and Faulwetter, 2018), but because it was just recently established, much trait information, such as that regarding larval development, is still in the process of being uploaded.

To assess the functional structure in the study area, we needed to select appropriate metrics to weigh the macrobenthos biological traits at each station. The BTA results based on both species abundance and biomass (afdm) show a clear separation in functional trait composition among the six subregions in the Bering Sea. In addition, the overall variability explained in the FCA on the basis of both approaches did not significantly differ, and the correlation ratios of the traits based on the two approaches were relatively high. Thus, both the abundance-based and biomass (afdm)-based BTA could be useful and informative tools to explore the changes in macrobenthic functional traits among the subregions in the study area. While Darr et al. (2014) considered that biomass is a more suitable parameter to describe macrobenthic community function than abundance, Gusmao et al. (2016) held the opinion that abundance-based BTAs represent an informative tool to describe the gradients in the functional trait composition of macrobenthos but that this was not the case for the biomass-based analysis. These contradictions could result from the use of different types and numbers of traits and from the distinct nature of the environmental filters themselves. Kokarev et al. (2017) used species respiration rates, which combine the abundance, biomass and taxon-specific coefficient, as the weighting values to explore the functional patterns of macrobenthic communities in the Laptev Sea. However, the estimation of the

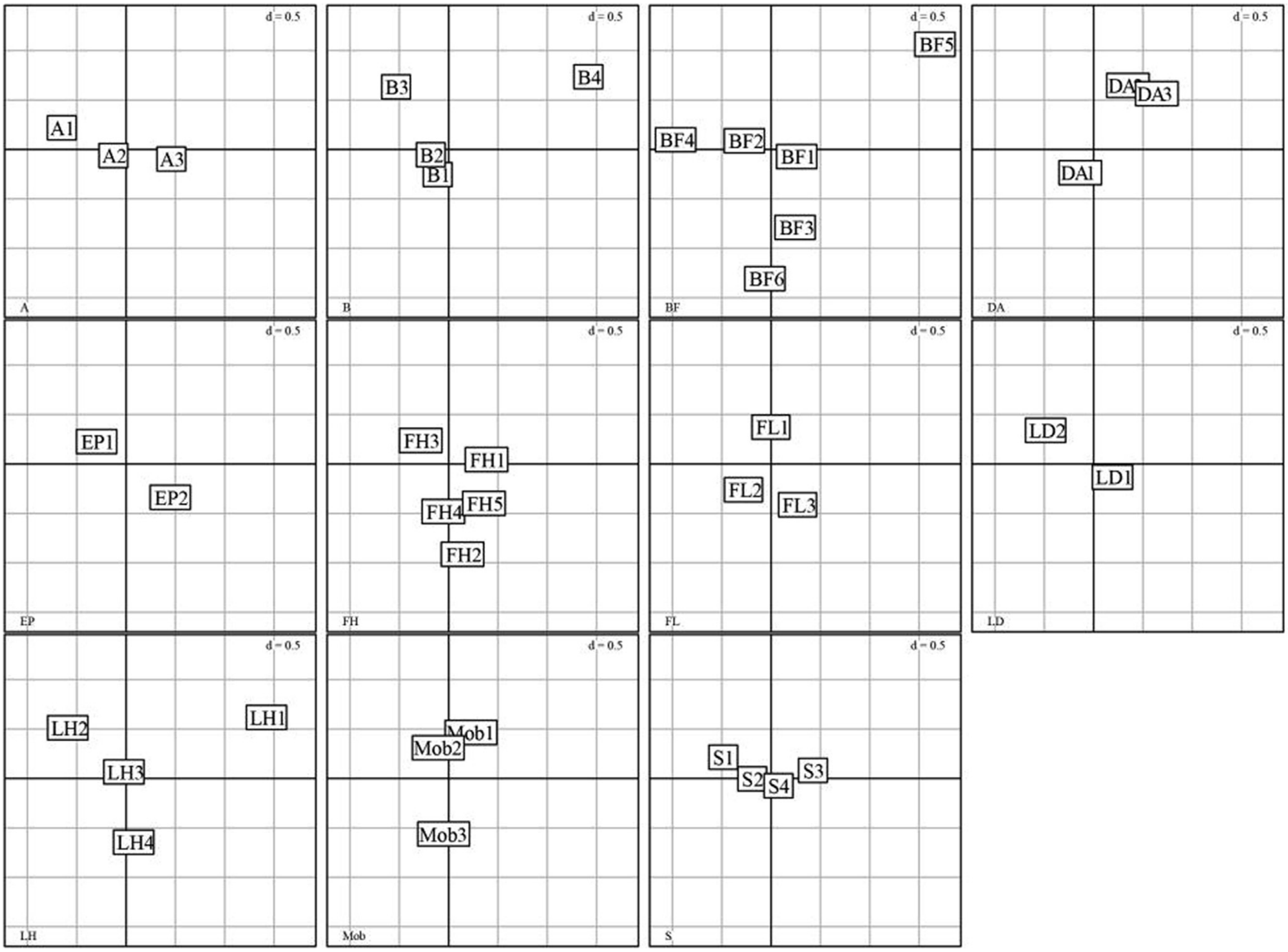

Fig. 7. Two-dimensional FCA plots weighted by biomass (afdm) showing the distribution of the trait modalities. See Table 1 for labels.

coefficient only occurred at a high taxonomic level (Class level), and differences among genera and species were neglected. These uncertainties, e.g., on the basis of the type and number of traits or functional groups used and the weighting of traits, potentially affected the results of the respective trait study in the Arctic, and we suggest that solutions to this issue should be considered in future research.

4.2. Patterns in functional traits across the Bering Sea shelf, shelf break and basin systems

There are significant differences in the species composition and distribution of macrobenthos along a shelf-slope-basin transect in the Bering Sea, and the community structure exhibits a dispersed and patchy distribution pattern. Depth and sediment composition are the main factors that obviously influence the structure of macrobenthic communities and the distribution of the dominant species (Lin et al., 2018). Similar to the variation in the taxonomic distribution and composition, the variability we observed in the biological trait distribution can be partly attributed to the habitat heterogeneity (e.g., related to the sediment composition or depth) that occurs in the study area. Grebmeier et al. (2006) revealed that sediment grain size and TOC, as the indirect indicators of current transport and sedimentation zones, affected macrobenthic functional structure.

Because of the influences of the Yukon and Kuskokwim rivers, a large amount of coarse terrigenous grain component is imported onto the north-eastern shelf of the Bering Sea. Meanwhile, the high flow velocity at the mouth of the Bering Strait transports fine sediments away, which results in a high proportion of sand in this area (Smith and McConnaughey, 1999; Grebmeier et al., 2006). The dominant species of the EB and NB, such as the polychaete *Scoloplos armiger*, crustaceans *Pagurus pubescens* and *Maera danae*, and echinoderm *Echinarachnius parma*, were typical of the ‘well-sorted fine-sand biocoenosis’. Our results show that most species in the EB and NB are mainly carnivores/omnivores or deposit feeders. However, Paganelli et al. (2012) reported that the macrobenthic community of sandy sediments is usually dominated by suspension feeders, whereas that of muddy sediments is dominated by detritus feeders. Rand et al. (2018) suggested that high current velocities tend to contain high loads of suspended particles that serve as food for these suspension feeders. The possible reason for this divergence could that the EB was influenced by fresher (< 31.8), more nutrient-limited Alaska Coastal Water, the productivity of the upper and middle water layers was low, and the suspended particle content was relatively lower, which leads to an insufficient food supply for suspension feeders.

The NB is typically covered in ice for five to six months of every year, which is presumably a period of little or no primary production (Grebmeier et al., 2006). The region, as an important habitat for grey whales, is dominated by amphipods and bivalves living in sandy mud (Moore and Laidre, 2006). However, in the past several decades, due to the influence of the earlier retreat of the seasonal sea ice and warming temperatures, the grey whale feeding sites have shifted from the northern Bering Sea northward to as far as Barrow off the North Slope of Alaska (Moore and Laidre, 2006; Moore et al., 2003), and the benthic ecosystem has been changing in the NB. The dominant species in the NB changed from the tube-dweller and suspension feeder *Ampelisca macrocephala* to the surface crawler and deposit feeder/carnivore *Maera*

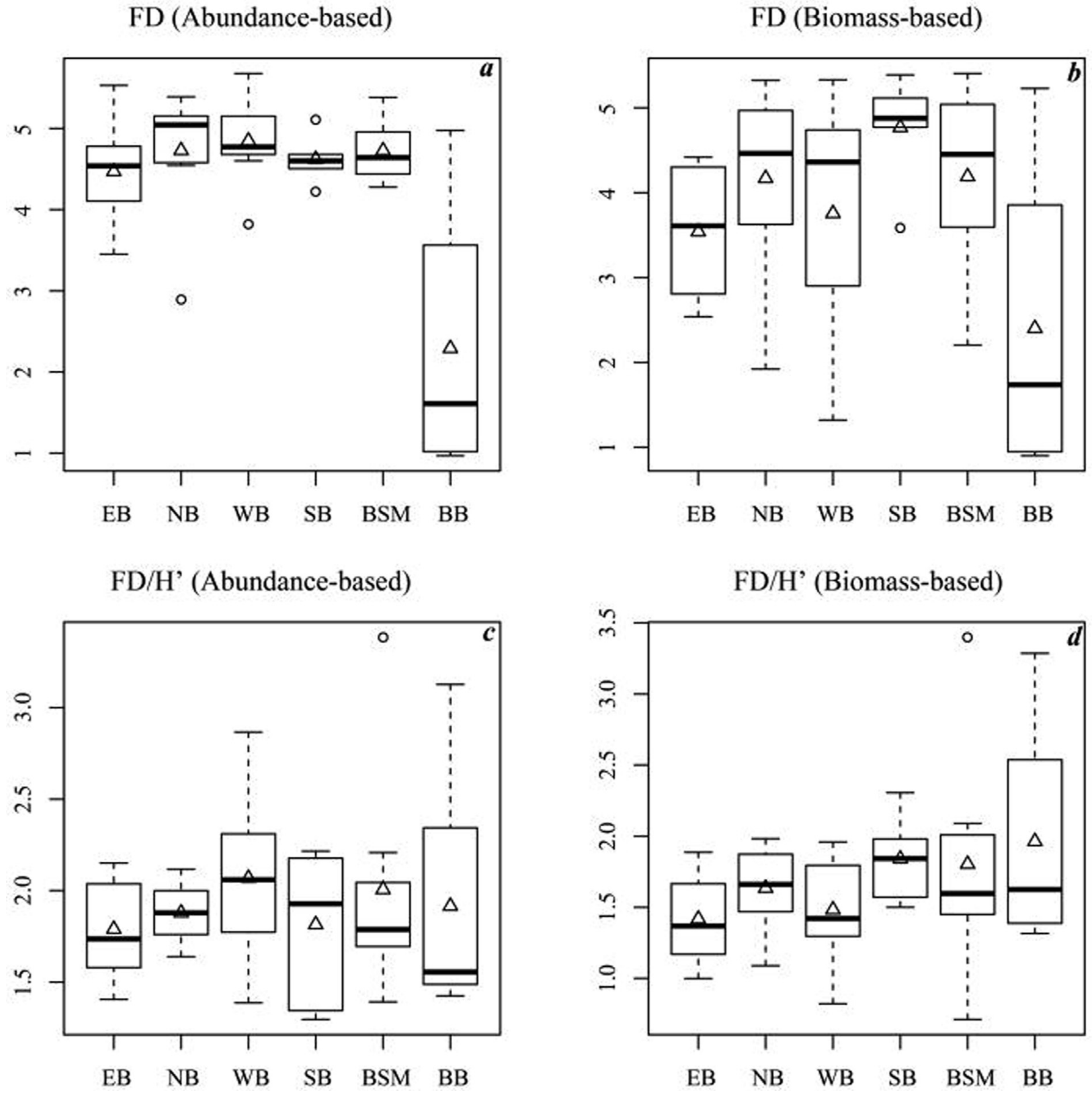

Fig. 8. Boxplots of FD and FD/H' based on abundance and biomass (afdm) in the six subregions. The small triangles and open circles represent the average values and outliers, respectively.

danae. The large burrower and deposit feeder/scraper *Echinarachnius parma* once was distributed in a band northeast of St. Lawrence Island between Bering Shelf-Anadyr Water and Alaska Coastal Water (Stoker, 1978). However, this species was not identified in this area in the study and was only found at one station (4-BS02) northwest of St. Lawrence Island.

As a persistent 'hot-spot' zone, the southwest region of St. Lawrence Island is characterized by high macrobenthic biomass, high sediment organic carbon and high silt content. The WB, SB and BSM are under the influence of more saline, nutrient-rich Anadyr Water and Bering Shelf Water, as indicated by the comparatively high abundance of polychaetes and echinoderms, which are characteristic of the 'mud biocoenosis'. These three subregions were grouped together along the first FCA axis based on abundance and the second FCA axis based on biomass (afdm), indicating that they are characterized by the prevalence of species with high body flexibility, vermiform, tube-dweller/burrower modalities (e.g., *Axiothella catenata* and *Scoloplos armiger*) or large, semi-motile, deposit feeder and flattened dorsally modalities (e.g., *Ctenodiscus crispatus* and *Ophiura sarsii*).

In this study, Zoanthidae und. and *Gersemia rubiformis* were identified in the WB. Normally, macrobenthic communities dominated by upright, temporary, sessile and suspension-feeding cnidaria are not common in this subregion. These two species were only found at station 14NB12, which had a considerably high sand content (sand % = 76.2%). This station is located in the middle of the Anadyr Strait and west of St. Lawrence Island. The high productivity of Anadyr Water and the flux of organic carbon to the bottom supported a rich macrobenthic community in this area (Grebmeier et al., 2006). Meanwhile, the Anadyr Strait has strong currents and sediment composed of a mixture of coarse pebbles and rocks, which benefit suspension feeders.

Small/small-medium-sized taxa, mainly polychaetes and amphipods, dominated the macrobenthic communities in the deep Bering basin, while these taxa were more evenly distributed in other subregions. Water depth is the main factor inhibiting the downward transport of particulate organic carbon in the Bering basin. The insufficient food sources thus result in relatively low species diversity and

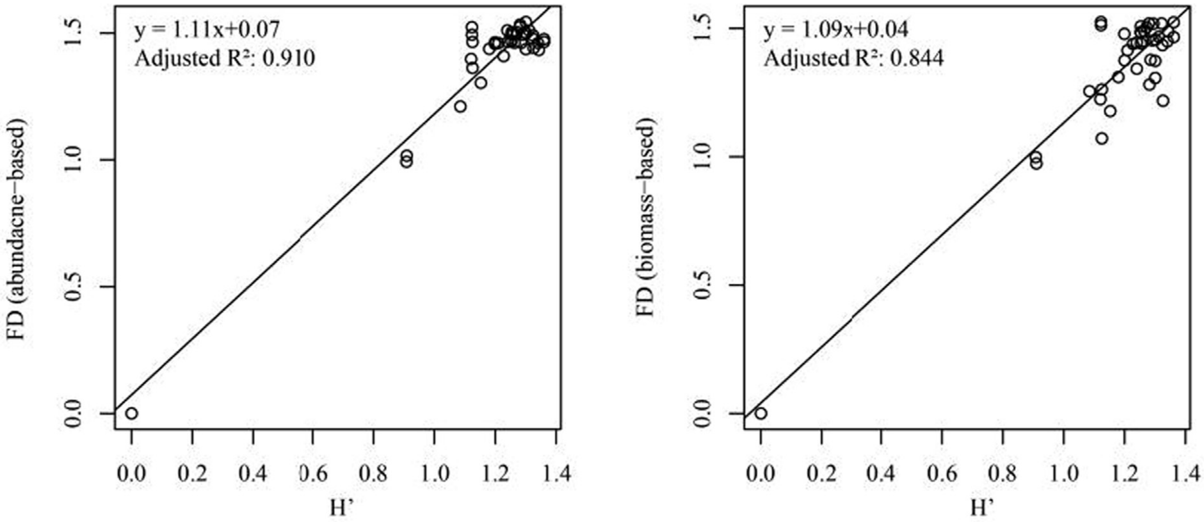

Fig. 9. Relationships between functional and species diversity (four root transformation) based on abundance and biomass (afdm) across 39 sampling locations in the Bering Sea.

FD of macrobenthos in this subregion. Such characteristics have been described previously in other Arctic deep-sea regions, such as in the Amundsen basin (Degen, 2015).

4.3. Relationship between taxonomic and functional diversity

No significant divergence in FD was found along the analysed environmental gradient (Van Der Linden et al., 2012; Darr et al., 2014). The results of this study show a similar pattern: the FD remained relatively stable along the depth gradient regardless of whether the analysis was based on abundance or biomass.

It is commonly assumed that changes in species diversity lead to changes in FD, but the relationship between these two community properties remains largely unknown for most ecological systems (Naeem and Wright, 2003). Frid and Caswell (2015) suggested that trait composition showed certain variability in three multi-decadal time-series but that the pattern of the changes in trait composition did not correspond to that of the changes in taxonomic composition. However, Micheli and Halpern (2005) and Kokarev et al. (2017) found a significant linear relationship between the species diversity and FD of macrobenthos. Rich species pools with high functional redundancy ensure the relative independence of community functions from species turnover over space and/or time. The data in our study also show an apparent linear relationship between species diversity and FD. This result potentially indicates that the macrobenthos community exhibits relatively low functional redundancy in the Bering Sea and that the benthic ecosystem is vulnerable to species loss or regime shifts.

5. Conclusions

This is the first study to describe the composition and diversity of macrobenthic biological traits across the Bering Sea. Although the results were influenced by high variability due to the consideration of different gradients, the shifts of the functional composition of macrobenthos along the sediment particle size and depth gradient were dominant. In addition, variation patterns derived from the abundance-based and biomass-based metrics were evident. The macrobenthos of the shallow, north-eastern shelf, which has sandy sediment, was largely composed of surface-crawling, motile and carnivore/scavenger taxa, while that of the deep, south-western shelf and shelf break, which have silty-sand sediment, was largely composed of taxa characterized by the high body flexibility, vermiform, tube-dweller/burrower modalities or large, semi-motile, deposit feeder and flattened dorsally modalities. The strong linear relationship between the species diversity and FD of the macrobenthos in the study area potentially indicates that relatively low functional redundancy occurs in these communities. Low functional redundancy makes the ecosystem less buffered and thus more susceptible to a species loss or structural shifts caused by environmental change. Therefore, we suggest applying BTA and functional redundancy index as a reliable approach to assess the effects of rapid ongoing changes on the functioning of marine polar ecosystems. This study will provide some basic data for the establishment of the Arctic macrobenthic traits database. Further diversity studies within the Arctic region that incorporate aspects of both species identity and functional characteristics will prove useful for forecasting Arctic marine ecosystem change.

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