



FEATURE ARTICLE

Comparison of functional diversity of two Alaskan Arctic shelf epibenthic communities

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ABSTRACT: Alaskan Arctic shelf communities are currently experiencing dramatic changes that will likely affect ecosystem functioning of Arctic marine benthic communities. Here, functional diversity based on biological traits was used to assess differences and similarities in ecosystem functioning between 2 shelf systems that are geographically close but vary in many environmental influences: the Arctic Beaufort and Chukchi Sea epibenthic communities. We hypothesized that (1) patterns of functional composition and diversity metrics reflect patterns in taxonomic composition and diversity metrics in these 2 shelf communities; and (2) patterns in functional diversity metrics are distinct between the 2 shelves. We evaluated 9 biological traits (body form, body size, feeding habit, fragility, larval development, living habit, movement, reproductive strategy, sociability) for 327 taxa in 2014 and 2015. For each trait, multiple modalities (specific expressions within a trait) were considered. Patterns in functional diversity metrics on both shelves reflected those in taxonomic diversity metrics. However, shelf communities were more similar in functional- than in taxonomic composition. Beaufort Sea communities had higher functional dissimilarity and functional evenness driven by differences in the modalities within body form, body size, larval development, and reproductive strategy. These traits primarily affect nutrient cycling, energy turnover, and recovery from disturbances, suggesting a stronger potential for future maintenance of ecosystem function, and indicating a more even use of resources in the Beaufort Sea. The combination of functional and taxonomic diversity metrics enabled a comprehensive understanding of how ecological niche space is used and how epibenthic communities function in Alaskan Arctic shelf systems.



Differences in functional diversity and functional composition of epibenthic invertebrate assemblages on Alaskan Arctic shelves lead to differences in ecosystem functioning.

Photo: Katrin Iken

KEY WORDS: Biological traits · Biodiversity-ecosystem-functioning (BEF) · Niche space · Resource use · Invertebrates

1. INTRODUCTION

Arctic ecosystems are changing rapidly as the Arctic is warming twice as fast as the rest of the planet (Stroeve et al. 2012), with continued decreases in sea ice extent (Carmack et al. 2016) and changes in primary production (Arrigo & van Dijken 2015, Frey et al. 2019). Ongoing shifts in the Arctic environment are associated with changes in marine community

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[§]Corrections were made after publication. Fig. 5 was re-drawn for better clarity. The data did not change.
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composition and ecosystem processes (Huntington et al. 2020, Waga et al. 2020). For example, environmental changes, such as changes in temperature or sea ice, can increase stress for Arctic species but create habitat conditions suitable for northward-moving boreal species, thus changing community composition (Mueter & Litzow 2008, Thorson et al. 2019). Alaskan Arctic shelves are known for regionally high productivity and tight pelagic–benthic coupling, leading to some of the most productive benthic shelf areas in the world (Grebmeier et al. 2006). Arctic benthic assemblages within the Beaufort and Chukchi Sea shelf communities are of great importance for these ecosystem processes, as they support important food webs, which can channel anthropogenic or climatic perturbations to upper trophic levels (Iken et al. 2010, Divine et al. 2015). These benthivorous upper trophic levels include ecologically and socially important bearded seals, walruses (Fay 1982, Oliver et al. 1983), demersal fishes (Whitehouse et al. 2017), crabs (Divine et al. 2017), and birds (Lovvorn et al. 2003). Changes in benthic assemblages within shelf communities or in the energy pathways supporting these assemblages will therefore have effects on overall Arctic shelf ecosystem function.

Ecosystem function is broadly defined as the movement or storage of energy or material within an ecosystem (Bellwood et al. 2019). Benthic communities play important roles in ecosystem functions such as nutrient cycling (Kristensen 2000), energy turnover (Hall et al. 2009), trophic transfers (Iken et al. 2010), remineralization (Ambrose et al. 2001), and resuspension of sediments (Snelgrove et al. 2000). Although different Arctic benthic shelf communities may share these general functions, adjacent communities such as on the Beaufort and Chukchi Sea shelves—that differ distinctly in their oceanographic setting and primary production levels (Sakshaug 2004, Carmack & Wassmann 2006)—can be expected to differ in the specific functional roles the benthos plays. The Chukchi Sea is a shallow inflow shelf (*sensu* Carmack & Wassmann 2006), characterized by high nutrient influx from the Bering Sea, leading to high primary production. In contrast, the Beaufort Sea is a narrow interior shelf, which has lower primary production than the Chukchi Sea, driven by lower nutrient supplies from the Chukchi Sea to the western Beaufort shelf, upwelling from the shelf break, and high freshwater influx from the Mackenzie and Colville Rivers (Hill et al. 2013, 2018, Grebmeier & Maslowski 2014). These differences in key environmental influences are suspected to play a role in driv-

ing patterns in taxonomic composition (e.g. Rand et al. 2018) and may also lead to differences in functional composition through differences in biological traits between the Beaufort and Chukchi Sea shelf benthic communities. This could result in different ecosystem functioning between the 2 shelves, despite their proximity. Consequently, the responses and resilience (i.e. the ability of communities to maintain ecosystem function) of the benthic communities to perturbations will likely differ between the Beaufort and Chukchi Sea shelves.

Functional diversity within a geographical area can help explain and predict regional ecosystem functioning and ecosystem resilience to environmental change. The Beaufort and Chukchi Sea epibenthic communities can be functionally described by ‘what they do’ based on specific functional traits of the taxa within the community rather than ‘who they are’ purely based on taxonomy (Petchey & Gaston 2006). Hence, functional diversity is defined as the range of organismal traits of species within a community that, combined, determines ecosystem functioning (Tilman 2001, Bremner et al. 2006). Different taxa can play a similar functional role in a community based on their traits. Conversely, taxonomically similar organisms can have different functions within a community (Hewitt et al. 2008, Krumhansl et al. 2016). Differences in biological trait expression within a community will lead to differences in resource use because biological traits represent how taxa extract and move resources in their environment (McGill et al. 2006, Cadotte et al. 2011). In essence, functional diversity is the balance of the roles of taxa within communities through different traits and through redundancy or complementarity of shared traits that influence overall ecosystem functioning (Díaz & Cabido 2001).

Arctic marine communities are at particular risk of experiencing competitive disadvantages relative to invading boreal species. Although Arctic taxa typically occupy a narrow temperature range, modeling studies suggest these taxa may be resilient to environmental pressures, including high temperatures (Renaud et al. 2015, 2019). Therefore, there is a need to better understand the resilience of these Arctic shelf communities to ongoing changes in the environment. In a resilient system, a specific ecosystem function would be maintained even if one or several taxa were removed from the system. High functional redundancy, where the same biological traits are represented by several different species within a community, and high functional diversity, where many different traits are represented by taxa within

a community, presumably lead to high ecosystem stability and increased resilience to change or disturbance (Hewitt et al. 2008).

The biodiversity–ecosystem–functioning (BEF) hypothesis states that higher taxonomic diversity leads to improved ecosystem functioning through diversified resource use, which ultimately leads to higher ecosystem stability (Loreau et al. 2001, Cardinale et al. 2009, 2012). This theory is based in an understanding of biodiversity from a taxonomic perspective, which for epibenthos has been established in recent years for the Beaufort and Chukchi Sea shelf study areas (e.g. Bluhm et al. 2009, Blanchard et al. 2013, Ravelo et al. 2014, 2015, 2020). The underlying assumption of the BEF hypothesis is that higher taxonomic diversity also reflects higher functional diversity, but these assumptions are rarely explicitly tested. Support for this underlying assumption, for example, has been found for the macrobenthos in the Bering Sea (Liu et al. 2019). Despite a long-standing and ongoing debate in the marine ecology scientific community of this concept (Naeem et al. 1994), few studies have analyzed the relationship between taxonomic diversity and ecosystem function in Arctic benthic marine systems (but see Kokarev et al. 2017, Rand et al. 2018, Liu et al. 2019), systems that are prone to perturbations. We contend here that, if the BEF assumption is correct, functional diversity on the 2 Arctic shelf communities should follow the same patterns as taxonomic diversity, as functional diversity is based in biological traits that are defined by a species' identity. However, if functional diversity provides a complementary perspective to ecosystem functioning that taxonomy alone does not provide, then a more comprehensive understanding of ecosystem function can be expected when functional diversity is analyzed alongside taxonomic diversity. Therefore, given distinct environmental influences on the 2 shelves, we hypothesized that (1) differences in functional composition and diversity metrics in epibenthic shelf communities reflect patterns in taxonomic composition and diversity metrics; and (2) patterns in functional diversity metrics of Beaufort and Chukchi Sea epibenthic shelf communities are distinct from each other.

2. MATERIALS AND METHODS

2.1. Study sites

Epibenthic invertebrates were collected during 4 cruises in 2014 and 2015 on the US Beaufort and Chukchi Sea shelves (Fig. 1). Here, we define each station as a representative assemblage of taxa within each shelf community. Beaufort Sea assemblages from 46 stations were studied during 3 research cruises: The US–Canada Transboundary Project 2014 sampled the central Beaufort Sea shelf, and the Arctic Nearshore Impact Monitoring in Development Area project III (ANIMIDA 2014, 2015) sampled the central and eastern Beaufort Sea shelf. Stations between 9 and 64 m bottom depth were included in this study. Chukchi Sea shelf assemblages from 67 stations were sampled during the Arctic Marine Biodiversity Observing Network survey in 2015 (AMBON 2015). These stations were sampled between 11 and 54 m bottom depth.

2.2. Sample collection

Epibenthic invertebrate assemblages were sampled during all cruises towing a 3.05 m wide plumb-staff beam trawl with a 2.6 m wide and 1.2 m high mouth opening with a 7 mm mesh and a 4 mm codend liner (modified after Gunderson & Ellis 1986).

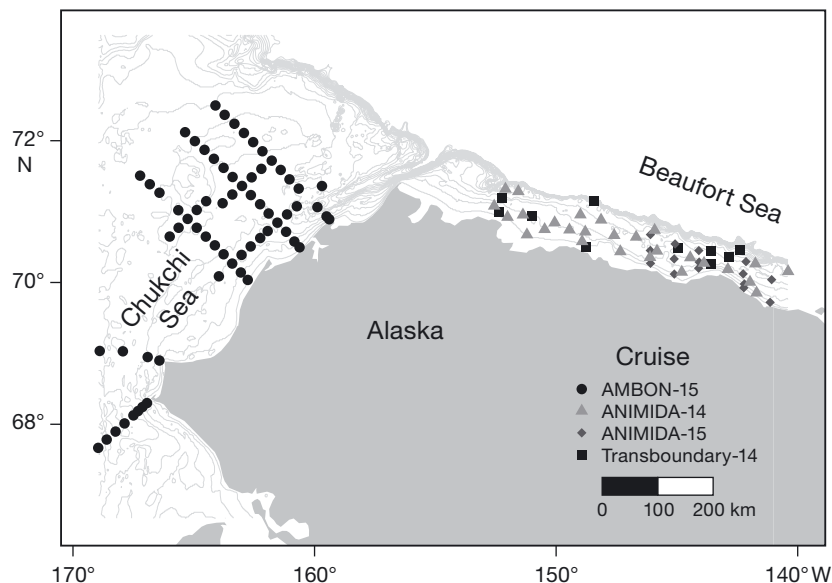


Fig. 1. Stations sampled for epibenthic communities during 4 cruises in the Beaufort and Chukchi Seas in 2014 and 2015. Stations are designated by symbols to different cruises. Depth contours in the study regions are shown in gray at 10 m intervals

Average trawl time at the bottom was 4–5 min at approximately 1.5–2 knots, depending on station depth and bottom conditions (see details in Iken et al. 2019). Biomass of all epibenthic invertebrates at each station was calculated as catch per unit effort by multiplying the estimated distance trawled by the width of the net and normalized to g wet weight per 1000 m². Bottom contact was determined using a time–depth recorder (Star Oddi). Invertebrates were identified onboard to the lowest feasible taxonomic level, and net wet weight of each taxon was recorded using digital hanging scales. Vouchers for taxa not identified in the field were fixed in either 10% formalin solution or 190-proof ethanol for later identification with the help of taxonomic experts listed in the acknowledgment section. Taxon names followed those in WoRMS (www.marinespecies.org) to standardize nomenclature.

2.3. Biological traits analysis

A dataset of biological traits was compiled for a total of 327 epibenthic taxa collected from both shelves. These data can be accessed via Table S1 in the Supplement (at www.int-res.com/articles/suppl/m651p001_supp.xlsx) and with references via The Arctic Traits Database (<https://www.univie.ac.at/arctictraits/>). The Beaufort Sea community consisted of 246 taxa and the Chukchi Sea community consisted of 247 taxa, with 166 shared taxa within these shelves. Taxonomic resolution varied for these taxa, but was similar between the 2 shelf communities. The Beaufort Sea had 163 and Chukchi Sea had 172 taxa identified to species, 60 and 56 to genus, 7 and 5 to family, 4 and 5 to class, 7 and 4 to order, and the same 5 taxa were identified at the phylum level (Table S1). Taxonomic identifications were based on the same taxonomic expertise (see Acknowledgements), so that the similar taxonomic resolution of the 2 sea shelf systems enabled an unbiased comparison of functional diversity based on biological traits. Biological traits analysis (BTA) functionally characterizes epibenthic organisms based on morphology, life history, and behavior. The BTA included a total of 9 traits related to morphology (body form, body size, fragility, sociability), behavior (feeding habit, living habit, adult movement), and life history (larval development, reproductive strategy), following the definitions and categories used by Degen & Faulwetter (2019) (Table 1). The biological traits matrix was assembled through a combination of qualitative traits based

on observations and our collective knowledge of Arctic invertebrates (morphological traits) and traits derived from extensive literature research (life history traits, behavioral traits). Where specific literature for a species was unavailable, traits were inferred from closely related species. Each trait was further separated into modalities to account for distinct categories within a trait that an organism could express (Table 1, Table S1).

The BTA was done with a fuzzy-coding approach, which allowed taxa to be assigned multiple modalities within a trait based on their affinity to those modalities (Chevenet et al. 1994, Bremner et al. 2006). Using a 0–3 scoring system, where 0 means no affinity and 3 is a high affinity to a modality, each taxon was assigned a number based on its affinity to each modality within a trait (Table S1, Chevenet et al. 1994). Taxa with equal affinity to several modalities within a biological trait were assigned the same score for those modalities. All fuzzy-coded modality scores within a trait were then weighted so that they summed to 1 for each taxon and trait. The scores for all modalities across all traits created unique taxa biological trait profiles (taxa by trait matrix). These matrices were multiplied by the relative taxa biomass at each station (taxa by station matrix) to create fuzzy-coded community weighted means (CWMs) for each station and trait. Therefore, the resulting station by trait matrix essentially highlighted the most common categorical modalities at each station, and therefore each assemblage, through biomass weighting (Table 2) (Garnier et al. 2007).

2.4. Shelf comparisons of functional and taxonomic diversity metrics

Five functional diversity metrics were calculated for the Beaufort and Chukchi Sea shelf epibenthic assemblages to enable a community-level comparison (Table 2). Each of the functional diversity metrics represented a unique facet of overall functional diversity (Mason et al. 2005, Mouchet et al. 2010). These included functional dissimilarity (Rao's quadratic entropy [Rao's Q]), functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), and functional redundancy (FRed = 1 – mean pairwise distances [MPD]) (Table 2). Functional dissimilarity (Rao's Q) compares how similar the biological trait profiles of taxa are to each other among assemblages (Rao 1982). Functional dissimilarity was complemented by functional metrics that described

Table 1. Biological traits and modalities assembled for epibenthic invertebrates collected in the Chukchi and Beaufort Seas, following Degen & Faulwetter (2019). Abb: modality abbreviations used in figures

Biological trait	Modality	Abb.	Description	Ecological relevance
Body form	Globulose	BF1	Round	Ecological role of species (e.g. habitat forming) and/or vulnerability to mechanical disturbances
	Vermiform	BF2	Wormlike	
	Dorso-ventrally compressed	BF3	Flattened/encrusting	
	Laterally compressed	BF4	Thin	
	Upright	BF5	Body forms upward from seafloor	
Size (wet weight, g)	Small	BS1	0.01–0.1	Effect on productivity, energy flow, trophic and food web structure
	Small–medium	BS2	0.1–1.0	
	Medium	BS3	1.0–10	
	Medium–large	BS4	10–100	
	Large	BS5	>100.0	
Feeding habit	Deposit feeder	FH1	Removes detrital material from sediment	Indicative of hydrodynamic conditions and carbon transport
	Filter/suspension feeder	FH2	Filters food from the water column	
	Opportunist/scavenger	FH3	Scavenges food	
	Predator	FH4	Actively hunts live prey	
	Parasite	FH5	Feeds off other organisms	
Fragility	Fragile	F1	Easily damaged due to physical impacts	Sensitivity to physical and/or predatory disturbances
	Intermediate	F2	Moderately damaged due to physical impacts	
	Robust	F3	Unlikely damaged due to physical impacts	
Larval development	Planktotrophic	LD1	Larvae feed and grow in water column	Ability to disperse, become invasive, or recover from disturbance
	Lecithotrophic	LD2	Larvae with yolk sac, pelagic for short periods	
	Direct development	LD3	No larval stage (eggs develop into juveniles)	
Living habit	Free living	LH1	Not limited to any restrictive structure	Vulnerability to predation and perturbations, habitat facilitation, storage and movement of energy
	Crevice dwelling	LH2	Inhabiting coarse/rock or algal holdfasts	
	Tube dwelling	LH3	Tube lined with sand, mucus, or CaCO ₃	
	Burrow dwelling	LH4	Inhabiting burrows in the sediment	
	Epi/endo zoic/phytic	LH5	Biogenic species or algal holdfasts	
	Attached	LH6	Adherent to a substratum	
Movement	Sessile/none	MV1	No movement as adult	Movement of energy through nutrient cycling, carbon deposition, and maintenance of habitat stability
	Burrower	MV2	Movement in the sediment	
	Crawler	MV3	Movement on surface via movement of appendages	
	Swimmer	MV4	Movement above the sediment	
Reproductive strategy	Asexual	R1	Budding	Ability to withstand disturbances and carbon transportation
	Sexual–external	R2	Eggs/sperm released into water	
	Sexual–internal	R3	Eggs deposited on substrate/internal fertilization	
	Sexual–brooder	R4	Eggs are brooded, larva/juvenile hatches	
Sociability	Solitary	SO1	Single individual	Sensitivity to disturbance and/or habitat forming
	Gregarious	SO2	Single individuals found in groups	
	Colonial	SO3	Living in permanent colonies	

Table 2. Summary of the functional indices used in this study, where N is the total number of species at each station, p_i and p_j are the relative biomass of species i and j , X_i is the fuzzy-coded trait value, d_{ij} is the dissimilarity in biological trait profiles for species i and j , $dist(i, j)$ is the nearest-neighbor minimum spanning tree (NMST) distance for each pair of species (i, j) , w_i and w_j are the proportional biomass of species i and j , T is the trait value (i.e. PCoA coordinates), n is the n^{th} trait value, Δd is the sum of biomass-weighted deviances from the center of gravity, $\Delta|d|$ is the absolute value of biomass-weighted deviances from the center of gravity, and dG is the mean distance to the center of gravity

Metric	Equation	Description	Ecology	Source
Community weighted mean (CWM)	$\sum_{i=1}^N p_i X_i$	Sum of the relative biomass-weighted species' biological trait profiles at a station	Functional composition at each station	Garnier et al. (2007), Laliberté & Legendre (2010)
Functional dissimilarity (Rao's Q)	$\sum_{i=1}^N \sum_{j=1}^N d_{ij} p_i p_j$	Biomass-weighted sum of mean trait dissimilarities between individuals within a station	Dissimilarity of species' biological trait profiles within a station	Rao (1982), Ricotta et al. (2016)
Functional evenness (FEve)	$\frac{\sum_{i=1}^{N-1} \left(\frac{PEW_i}{N-1} \right) - \frac{1}{N-1}}{1 - \frac{1}{N-1}}$	Cumulative Gower distances between pairs of species represented by the minimum spanning tree (MST) branch lengths that links all species for each station based on species' biological trait profiles	Resource use from the entire range of resources available	Mason et al. (2005), Villéger et al. (2008)
Partial weighted evenness (PEW)	$\frac{EW_i}{\sum_{i=1}^{N-1} EW_i}$			
Weighted evenness (EW)	$\frac{dist(i, j)}{w_i + w_j}$			
Functional richness (FRic)	$\frac{(T_1 + (1-T_1)j_1, T_2 + (1-T_2)j_2, \dots, T_n + (1-T_n)j_n)}{T_n + (1-T_n)j_n}$	Total convex hull volume of each station in functional trait space as defined by the PCoA axes	Total niche space occupied by the station	Villéger et al. (2008)
Functional divergence (FDiv)	$\frac{\Delta d + dG}{\Delta d + dG}$	Distribution of the biomass-weighted distances of species from the station center of gravity in functional trait space	Degree to which species differentiate within the niche space of a station	Villéger et al. (2008), Laliberté & Legendre (2010)
Functional redundancy (FRed; 1 - MPD)	$1 - \frac{1}{\sum_{i>j}^N p_i p_j d_{ij}}$	One minus the probability that species within a given station are equally and maximally different	Degree to which species play similar roles in communities	Rosenfeld (2002), Kembel et al. (2010), de Bello et al. (2016)

the available functional niche space (FRic) and how the space within a given niche was occupied among assemblages (FEve, FDiv) (Schleuter et al. 2010). As all traits were fuzzy-coded categorical variables, functional metrics of Rao's Q, FRic, FEve, and FDiv were based on a flexible distance-based framework (Laliberté & Legendre 2010). First, a Gower distance matrix among taxa was calculated using a trait by taxa matrix, followed by a principal coordinates analysis (PCoA). PCoA axes were then used as new 'trait values' to compute FRic, FEve, and FDiv for all stations (Laliberté & Legendre 2010). FEve used all PCoA axes, whereas FRic and FDiv used the maximum number of PCoA axes allowed where the number of taxa was greater than the number of traits. FRed represents the degree to which taxa play similar roles in communities, and was measured using the complement of MPD ($1 - \text{MPD}$) (Rosenfeld 2002, de Bello et al. 2016). All functional diversity metrics can range from 0–1, where 0 indicates low functional diversity and 1 indicates the highest possible functional diversity.

Functional diversity metrics were compared to complementary taxonomic diversity metrics (Table 3). Rao's Q was compared to the Simpson taxonomic-based diversity index (Simpson 1949). Simpson diversity measures the chance that 2 individuals within a station are from the same taxon. The Simpson diversity index equals the maximum value of Rao's Q if all taxa were functionally completely different (i.e. each taxon represents unique functions) and the Simpson index is, thus, commonly used in compar-

isons of functional and taxonomic diversity (Carmona et al. 2016). Margalef's richness index measures species richness while accounting for sampling effects, and was compared to FRic. Finally, Pielou's evenness index was used to calculate species evenness and was compared to FEve.

All diversity metrics were compared between the Beaufort and Chukchi Sea shelf communities using a linear model of the form:

$$y = \alpha + \beta \times d + \epsilon \quad (1)$$

where y is any of the diversity metrics, the intercept α corresponds to the mean value of index y for the Chukchi Sea, and d is a dummy variable with values $d = 0$ for the Chukchi Sea and $d = 1$ for the Beaufort Sea. Hence, the regression coefficient β corresponds to the mean difference in metric y between the Chukchi Sea and the Beaufort Sea. The error, ϵ , was modeled as a spatial random process with a correlation structure that exponentially declined with distance between stations to allow for spatial autocorrelation. This linear model form was chosen over a simple univariate test (e.g. ANOVA) due to the spatial nature of the residuals and the ability to account for spatial autocorrelation. Models were fit using a generalized-least-squares approach as implemented in the 'nmls' package in R (Pinheiro et al. 2017). If the autocorrelation term did not significantly improve the model fit, metrics were compared using a simple linear model fit via least squares. To further investigate the relationship between the number of taxa and functional diversity on each shelf, Rao's Q was com-

Table 3. Summary of the taxonomic-based metrics used in this study, where S_i is the biomass of species i , S is the total biomass of all species at each station, N is the total number of species at each station, and p_i is the relative biomass of species i at a station

Index	Formula	Description	Source
Simpson diversity index (D)	$1 - \sum_{i=1}^N \frac{S_i(S_i - 1)}{S(S - 1)}$	Equals the maximum value for Rao's Q if all species were completely functionally different (i.e. each species represents unique functions)	Simpson (1949)
Margalef's richness index (d)	$\frac{S - 1}{\ln(N)}$	Result of the number of species divided by the biomass of species at a given station	Magurran (2004)
Pielou's evenness index (J')	$\frac{H'}{\log(S)}$	Maximum possible value of the Shannon index (H')	Pielou (1975), Magurran (2004)
Shannon diversity index (H')	$-\sum_{i=1}^s p_i \ln(p_i)$	Proportion of species evenness relative to species biomass at a station	Shannon (1948)

pared to Margalef's index for the Beaufort and Chukchi Sea shelves using a non-linear generalized additive model (GAM).

2.5. Comparisons of functional and taxonomic composition

Significant differences in functional (based on CWM) and taxonomic composition (based on taxon biomass) between the Beaufort and Chukchi Sea shelf assemblages were determined with analyses of similarity (ANOSIM) using a Gower distance matrix for functional composition and a Bray-Curtis dissimilarity matrix for taxonomic composition (Clarke & Warwick 1994). No transformation was performed on the functional composition matrix, as this matrix was already fuzzy-coded for CWM. Taxon biomass data were square root transformed to balance the influence of rare and dominant taxa (Clarke & Warwick 1994). The 10 most influential taxa on taxonomic composition were compared between the 2 shelves (similarity percentages analysis, SIMPER). These taxa were further compared between shelves in percent total biomass, frequency of occurrence, and average percent biomass per station. Furthermore, functional composition based on the proportion of modalities within biological traits was compared between the Beaufort and Chukchi Sea shelf communities using a fuzzy correspondence analysis (FCA; Chevenet et al. 1994). To focus on biological traits that drove patterns in functional composition on each shelf, correlation ratios from the FCA were evaluated for the first 2 axes of the FCA. High correlation ratios indicate strong relationships of biological traits with the FCA axes. Following previous studies on biological traits (Conti et al. 2014, Kokarev et al. 2017), we considered biological traits with correlation ratios >0.1 as most representative of the variance captured by the FCA axes. All analyses evaluating differences in functional and taxonomic compositions were computed using the 'vegan' package (Oksanen et al. 2019) in R version 4.0.2 (R Core Team 2020). Functional and taxonomic composition for each shelf were compared using the RELATE routine in the Primer V.7 software package (Clarke & Gorley 2015). Sufficient permutations were possible for all comparisons, and statistical significance was set at $\alpha = 0.05$.

In addition to between-shelf comparisons, the relationships of functional and taxonomic structures were evaluated within each shelf using a multistep process of multivariate statistics. First, we investi-

gated which taxa and modalities best represented communities for each shelf using the BVSTEP analysis within the BEST routine in Primer V.7 (Clarke & Gorley 2015). Specifically, we investigated which subset of taxa or subset of modalities were necessary to maintain the original structures of taxonomic or functional composition and were therefore considered representative of the functional and taxonomic structure. These representative subsets of modalities and taxa were determined using a stepwise procedure based on at least 95 % Mantel correlations. Subsequently, these subsets were considered as characteristic taxa and influential modalities. Resemblance matrices from these characteristic species and influential modalities were then compared using RELATE tests for each shelf separately.

3. RESULTS

3.1. Functional and taxonomic diversity metrics

All diversity metrics except FRed had higher median values in the Beaufort Sea shelf community compared to the Chukchi Sea shelf community. However, only 2 functional diversity metrics (Rao's Q, FEve) and the corresponding taxonomic metrics (Simpson's diversity, Pielou's evenness) were significantly higher in the Beaufort than Chukchi Sea shelf community (Fig. 2, $p < 0.01$). No spatial autocorrelation was detected for Rao's Q, FRic, Simpson diversity, and Pielou's evenness, but was present in FEve, FDiv, Margalef's index, and FRed (Table 4). Fewer taxa were required to increase functional dissimilarity (Rao's Q) in the Beaufort Sea compared to the Chukchi Sea (Fig. 3).

3.2. Comparison in functional and taxonomic composition between shelves

The Beaufort and Chukchi Sea epibenthic shelf communities moderately differed in functional composition, despite substantial overlap (ANOSIM: $R = 0.292$, $p = 0.001$, Fig. 4a). The first 2 FCA axes accounted for 42.36 % of the total inertia, with 24.70 % explained by axis 1 and 17.66 % explained by axis 2 (Fig. 4a). The biological trait movement was mostly separated along axis 1, while fragility was mostly separated along axis 2 (Fig. 5). The biological traits body form, body size, larval development, and reproductive strategy were strongly correlated with both axes, with correlation ratios ≥ 0.1 (Table 5, Fig. 5).

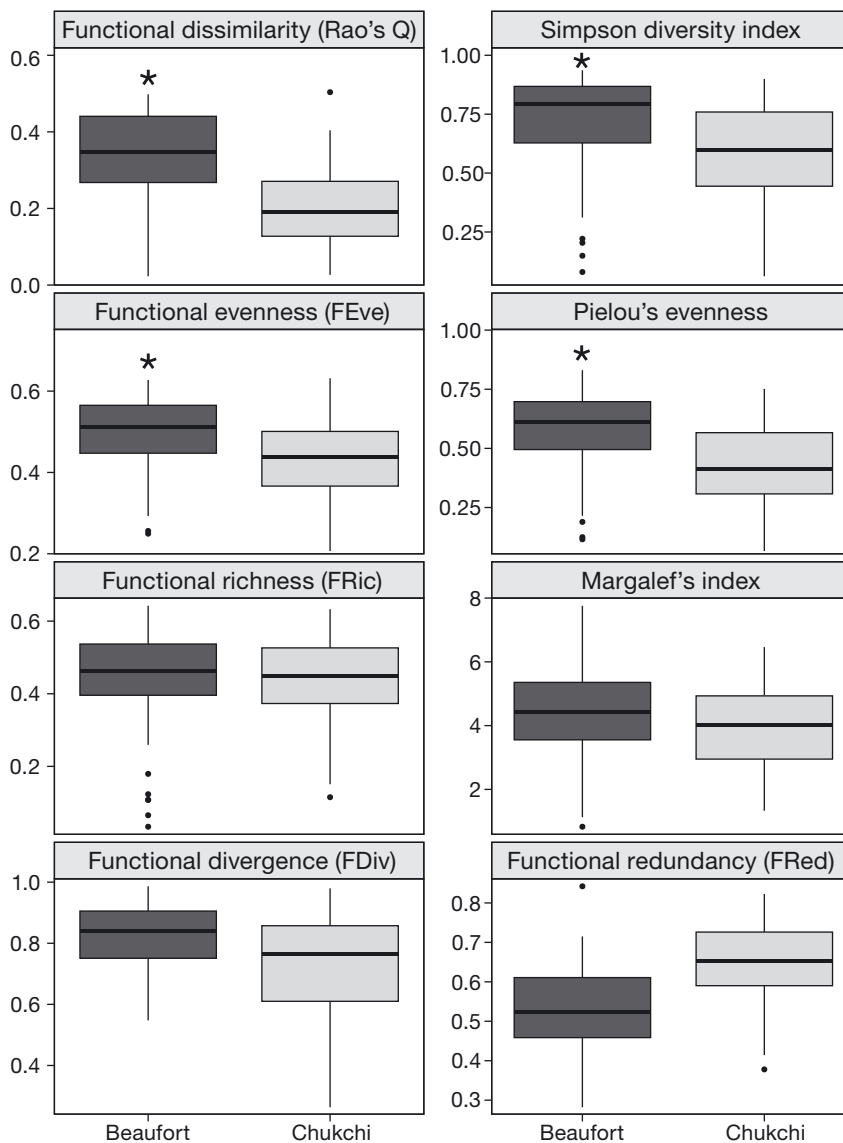


Fig. 2. Diversity metrics for the Beaufort (dark gray) and Chukchi (light gray) Sea shelf epibenthic assemblages based on community weighted means for functional diversity indices and square root transformed biomass for taxonomic diversity indices. Thick horizontal lines: median; boxes: inter-quartile range (IQR); whiskers: highest/lowest values $\leq 1.5 \times$ IQR above/below box; black points: outliers. *Significant difference between shelf assemblages (see Table 4)

Within these biological traits that strongly correlated with both FCA axes, the Beaufort Sea shelf assemblages had proportionally higher biomasses of globulose (BF1) and laterally compressed (BF4) body forms, lecithotrophic (LD2) and direct development (LD3), small-medium sized (BS2), and sexual-brooder (R4) modalities compared with Chukchi Sea assemblages (Fig. 6). Conversely, the Chukchi Sea shelf assemblages had proportionally higher bio-

masses of dorso-ventrally compressed (BF3) and upright (BF5) body form, planktotrophic development (LD1), medium (BS3) and medium-large size (BS4), and sexual-external (R2) modalities (Fig. 6).

The Beaufort and Chukchi Sea epibenthic shelf communities also differed in taxonomic composition (ANO SIM, $R = 0.676$, $p = 0.001$, Fig. 4b). The Beaufort Sea shelf contained 246 taxa and the Chukchi Sea shelf harbored 247 taxa, with a total of 327 unique taxa combined for the 2 shelves. Of the total taxa, 166 taxa (51 % of total) were shared between the Beaufort and Chukchi Sea shelf communities. The holothurian *Psolus peronii*, the scallop *Similipecten greenlandicus*, the brittle stars *Ophiocten sericeum* and *Ophiura sarsii*, the snow crab *Chionoecetes opilio*, the sand dollar *Echinarachnius parma*, the shrimp *Argis* sp., the basket star *Gorgonocephalus* sp., and the lyre crab *Hyas coarctatus* contributed most to differences in taxonomic composition between the 2 shelves (SIMPER, Table 6, Fig. 4b). The 2 shelf communities differed strongly in the taxa that contributed most to biomass and frequency of occurrence (FO) per shelf. The Beaufort Sea shelf community was dominated in total biomass, average biomass per station, and FO by *P. peronii*, *S. greenlandicus*, and *O. sericeum*. In contrast, the Chukchi Sea shelf community was dominated in total biomass and average biomass per station by *O. sarsii*, *C. opilio*, and *E. parma*, while FO was highest for *C. opilio*, *Argis* sp., and *H. coarctatus* (Table 6).

3.3. Comparison of functional and taxonomic composition within each shelf

Patterns in functional and taxonomic composition were significantly related to each other within both the Beaufort and Chukchi Sea shelf communities (RELATE test: $\rho = 0.497$, $p = 0.001$ for Beaufort Sea; $\rho = 0.619$, $p = 0.001$ for Chukchi Sea). Eight taxa best characterized the Beaufort Sea shelf taxonomic

Table 4. Metrics compared between the Beaufort and Chukchi Seas, model structure (with or without spatially autocorrelated residuals), estimated mean for the Beaufort Sea (intercept α), difference between Chukchi and Beaufort Sea means (β), and significance level for β . Significant differences ($p \leq 0.05$) in **bold**. Rao's Q: Rao's quadratic entropy (a measure of functional dissimilarity); FEve: functional evenness; FRic: functional richness; FDiv: functional divergence; FRed: functional redundancy; other indices are defined in Table 3

Metric	Spatial auto-correlation	α (CI)	β	Significance ($H_0: \beta = 0$)
Rao's Q	No	0.326 (0.294–0.358)	-0.126	<0.001
Simpson	No	0.707 (0.644–0.771)	-0.136	0.002
FEve	Yes	0.493 (0.449–0.053)	-0.056	0.053
Pielou	Yes	0.588 (0.503–0.672)	-0.137	0.020
FRic	No	0.431 (0.392–0.470)	-0.003	0.827
Margalef	Yes	4.501 (3.858–5.145)	-0.768	0.078
FDiv	Yes	0.793 (0.651–0.936)	-0.123	0.464
FRed	Yes	0.553 (0.461–0.644)	0.228	0.276

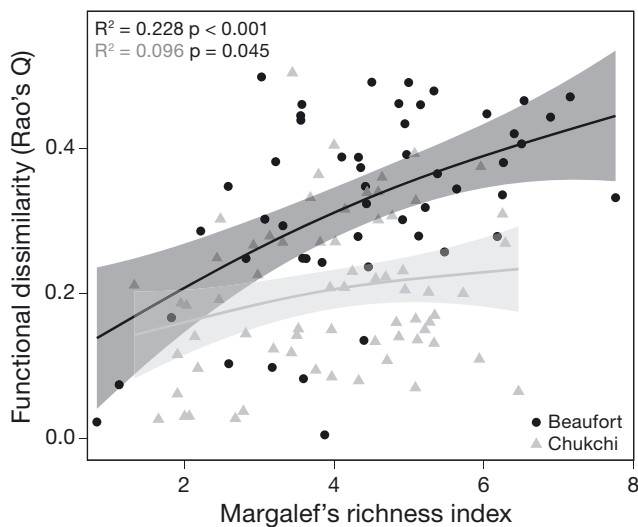


Fig. 3. Functional dissimilarity (Rao's Q) in the Beaufort Sea (dark gray) and Chukchi Sea (light gray) as a function of species richness (Margalef's index). Trends and confidence intervals estimated based on a generalized additive model (GAM) smoother to visualize the general trends

structure (BVSTEP, Spearman's correlation coefficient: 0.952, $p = 0.001$, Fig. 7a). These taxa were the amphipods *Acanthostepheia behringiensis* and *Paroedicerus lynceus*, the cumacean *Diastylis goodsiri*, the seastars *Leptasterias groenlandica* and *Urasterias lincki*, the brittle star *O. sericeum*, the holothurian *P. peronii*, and the shrimp *Sabinea septemcarinata*. Six modalities contributed most to the Beaufort Sea functional structure (BVSTEP, Spearman's correlation coefficient: 0.951, $p = 0.001$). These modalities were dorso-ventrally compressed (BF3), robust (F3), sessile (MV1), sexual-brooding

(R4), sexual-external reproduction (R2), and solitary (SO1). These influential modalities were well represented by the characteristic taxa (Fig. 7a). In this matrix of characteristic taxa by modality, 48% of the possible taxa-modality pairings reflected some affinity to each other, often even high affinity. Resemblance matrices of the subset of characteristic taxa and the influential modalities for the Beaufort Sea were significantly related (RELATE; $\rho = 0.569$, $p = 0.01$).

A larger subset of taxa and modalities were needed in the Chukchi than the Beaufort Sea community to maintain taxonomic and functional structure. We found that 28 taxa best characterized Chukchi Sea shelf taxonomic structure across all stations (BVSTEP, Spearman's correlation coefficient: 0.951, $p = 0.01$; Fig. 7b). Eleven modalities that most influenced the Chukchi Sea functional structure (BVSTEP, Spearman's correlation coefficient: 0.905, $p = 0.001$) were direct development (LD1), lecithotrophic development (LD2), fragile (F1), gregarious (SO2), solitary (SO1), laterally compressed (BF4), upright (BF5), medium size (BS3), predator (FH4), sessile (MV1), and swimmer (MV4). Influential modalities in the Chukchi Sea were expressed to a lesser degree (39%) by the characteristic taxa, and often at a lower affinity than in the Beaufort Sea (Fig. 7b). Resemblance matrices of the subset of characteristic taxa and influential modalities for the Chukchi Sea were significantly related (RELATE; $\rho = 0.517$, $p = 0.01$).

4. DISCUSSION

This study described the functional composition of the Beaufort and Chukchi Sea epibenthic shelf communities and explored the functional and taxonomic relationships between the 2 shelf systems. Overall, functional diversity patterns reflected those in taxonomic diversity on each shelf, supporting our first hypothesis. In addition, we found that the 2 shelves were functionally distinct, supporting our second hypothesis, albeit with much overlap in similar proportions of modalities between the 2 shelves. The biological traits that differed between shelves, especially those related to larval development, reproductive strategy, body size, and body form, can inform about energy flow and resource

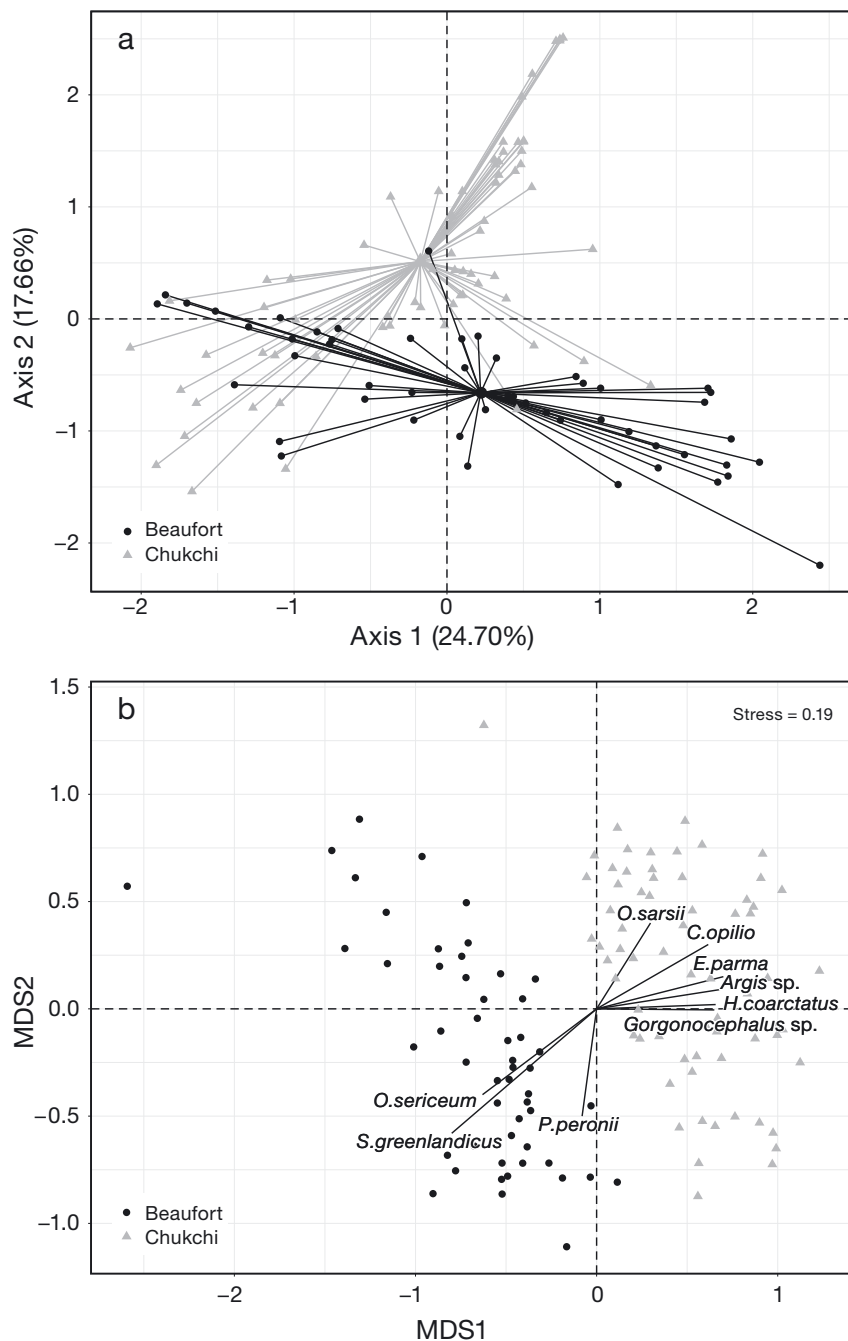


Fig. 4. (a) Fuzzy correspondence analysis (FCA) of functional composition and (b) non-metric multidimensional scaling (nMDS) plot of taxonomic composition of the Beaufort and Chukchi Sea shelf epibenthic communities. Each point represents a station in the Beaufort (dark gray) or Chukchi (light gray) Sea. Functional composition was based on the proportion of community-weighted-mean modalities expressed at each station, while taxonomic composition was based on square root transformed biomass. Vectors in the FCA (a) represent the distance of stations to the centroid for each shelf system. Vectors in the nMDS (b) represent taxa that contributed most to differences in taxonomic composition between the 2 shelves (SIMPER analysis). The direction of vectors in the nMDS indicates where taxon biomass increased and influenced the ordination, and vector length indicates the strength of the pattern in taxon biomass along that direction. Full species names are given in Table 5

partitioning within each shelf as well as different community responses to changes and disturbances (Rand et al. 2018). The overlap in functional composition, but strong separation of taxonomic composition between the Beaufort and Chukchi shelves, suggests that different taxa fulfill similar functions in the 2 systems. Therefore, functional analyses provided complementary perspectives that related the taxonomic patterns to ecosystem function on these Arctic shelves. Specifically, we can use dominant biological traits to pinpoint which resources (e.g. available food or space) are most affected by changes or perturbations in the available niche space, and how efficiently those niche spaces are occupied on these 2 shelf systems.

4.1. Comparison of taxonomic and functional diversity metrics

At the core of the BEF concept is the premise that higher taxonomic diversity leads to more efficient ecosystem functioning through higher interaction strength between taxa and their environment. The principle is that more species will use a more diverse set of resources in a system, ultimately increasing the stability of the system against perturbations (Loreau et al. 2001, Cardinale et al. 2009, 2012). In our study, taxonomic diversity (Simpson) and evenness (Pielou's) were significantly higher in the Beaufort Sea shelf assemblages compared to the Chukchi Sea shelf assemblages, but there was no difference in taxonomic richness (Margalef's index) between the 2 shelves. This similarity in taxonomic richness as well as in functional richness between the 2 shelf systems provided a unique opportunity to compare functional redundancy of the 2 shelves in similar taxonomic and functional space. Fewer modalities and fewer taxa were needed to describe the

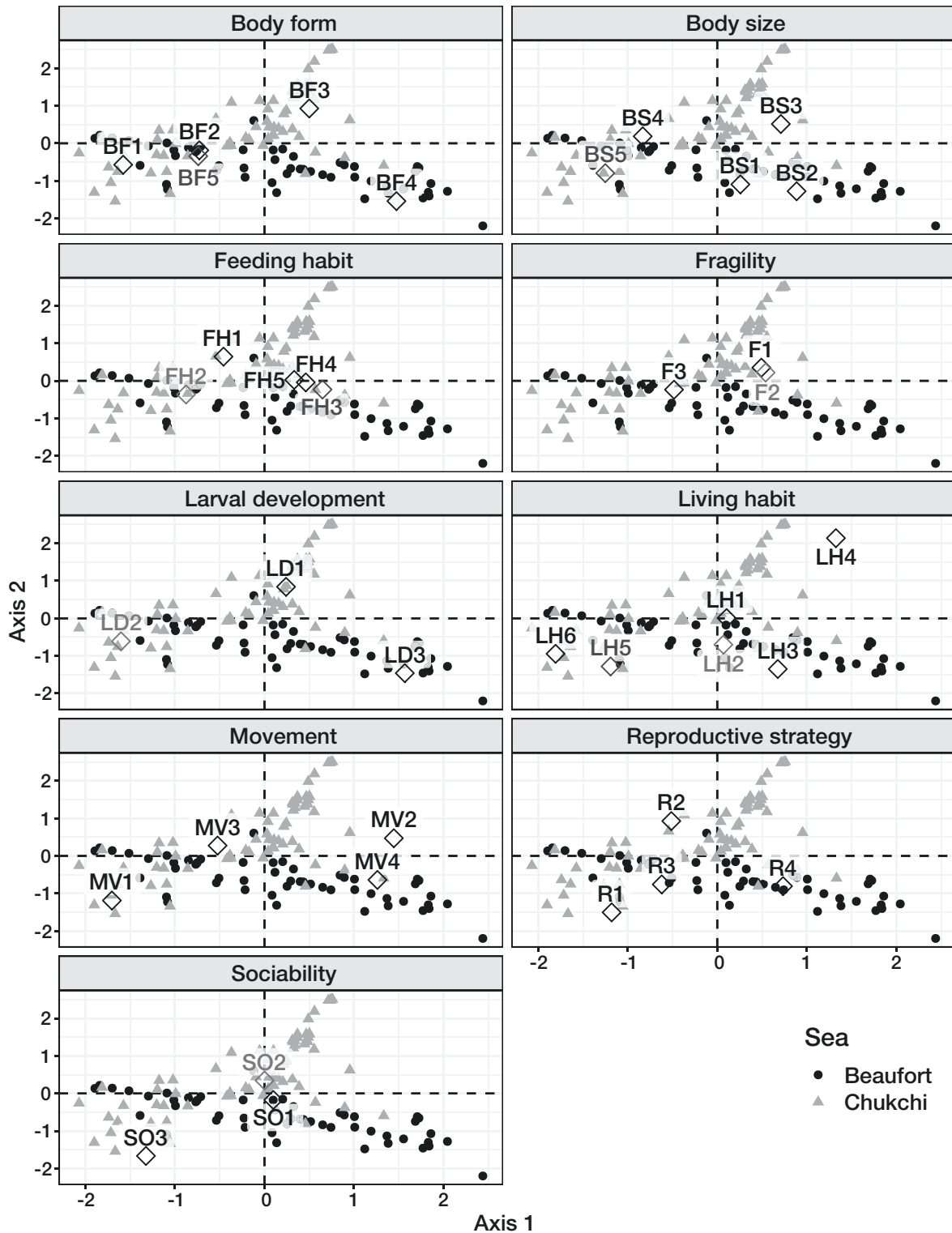


Fig. 5. Fuzzy correspondence analysis plots of functional composition for stations from the Beaufort (dark gray circles) and Chukchi Sea (light gray triangles) for all biological traits of epibenthic taxa. Modalities are denoted by diamonds with corresponding colors of abbreviated modality names. Position of the modalities is representative of association strength and influence on the ordination. For modality definitions and modality abbreviations see Table 1

Table 5. Correlation ratios of the biological traits for the first 2 fuzzy correspondence analysis (FCA) axes (see Fig. 4a). Biological traits (trait details in Table 1) that accounted for the most variation in the FCA (correlation values [RS] ≥ 0.1) are shown in **bold**

Trait	RS1	RS2
Body form	0.26	0.21
Body size	0.17	0.11
Fragility	0.06	0.12
Feeding habit	0.09	0.03
Larval development	0.30	0.22
Living habit	0.08	0.07
Movement	0.26	0.07
Reproductive strategy	0.10	0.19
Sociability	0.02	0.04
Variance (%)	24.70	17.66
Eigenvalues	0.15	0.11

relationships between taxonomic and functional composition of the Beaufort Sea community (8 taxa, 6 modalities) compared to the Chukchi Sea community (28 taxa, 11 modalities; see Fig. 7), reflecting a higher functional redundancy in the Chukchi Sea. Additionally, fewer taxa were required in the Beaufort Sea to increase functional dissimilarity compared to the Chukchi Sea at a given taxon richness. Together, these relationships point to lower functional redundancy and highly diverse biological trait profiles in the Beaufort Sea that tended to be dominated by single modalities within biological traits. High functional evenness in the Beaufort Sea indicated that most biological traits within assemblages were expressed evenly in functional space, albeit with individual taxa dominated by unique modalities. Likewise, the higher taxonomic evenness pointed to more evenly distributed biomass of taxa on the Beaufort Sea shelf. Our results show that, in general, functional diversity metrics measured on Alaskan Arctic shelf systems mirrored those of taxonomic metrics, following the hypothesized pattern of the BEF concept. Similar patterns between functional and taxonomic composition were found for the Bering Sea macrobenthos (Liu et al. 2019).

Given that species are the building blocks of ecosystem function (Bellwood et al. 2019), functional diversity can pinpoint which characteristics, or traits, of species diversity influence ecosystem function (Tilman 2001). For example, we saw strong differences between shelves in body size, likely affecting the movement of energy across the shelves,

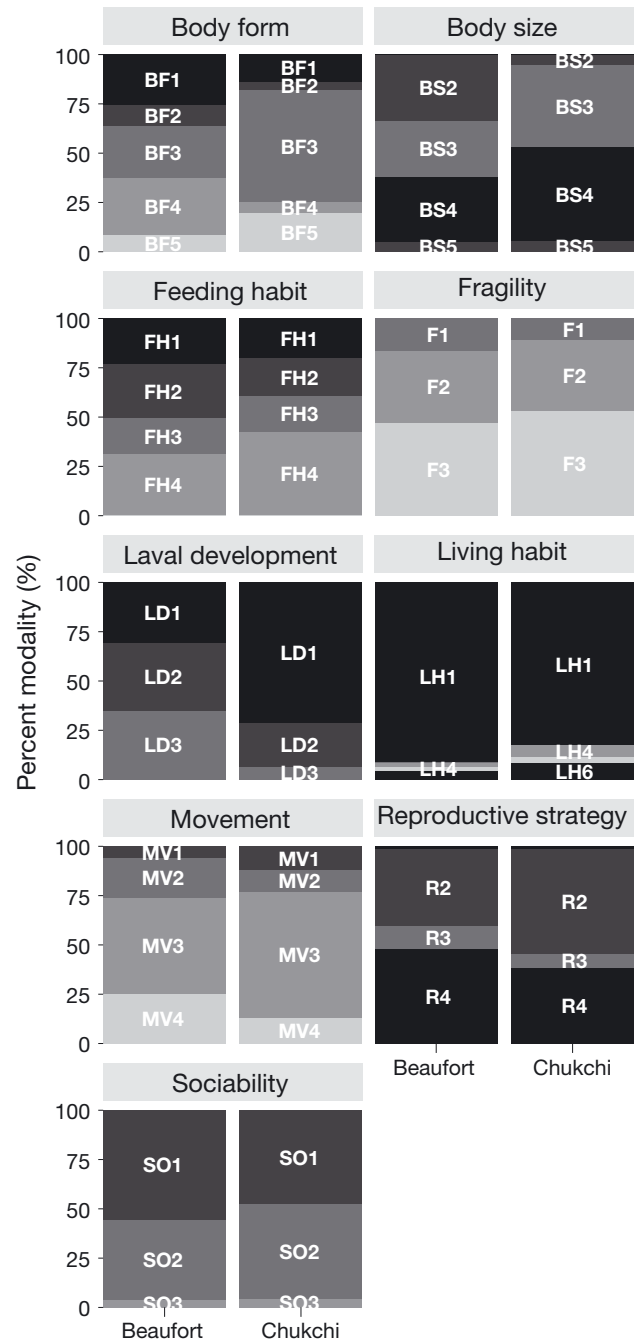


Fig. 6. Percent of each modality within each biological trait for the Beaufort (left bars) and Chukchi (right bars) Sea shelf epibenthic communities. Only modalities that contributed $>2\%$ of the total sea community weighted mean (CWM) biomass are shown. Modality abbreviations as in Table 1

and in larval development, reproductive strategy, and body form, all of which can inform about resistance to disturbances. This relationship between the 2 diversity approaches emphasizes the importance of using functional diversity as a com-

Table 6. Epibenthic taxa with the largest percent contribution to differences in taxonomic composition between the Beaufort (Beau) and Chukchi (Chuk) Sea shelves, ordered from highest to lowest contribution. The cumulative percent of total biomass for influential taxa is shown

Species	SIMPER results (%)		Total biomass (%)		Frequency of occurrence (%)		Average biomass per station when present (%)	
	Indiv. contrib.	Cum. contrib.	Chuk	Beau	Chuk n = 67	Beau n = 52	Chuk n = 67	Beau n = 52
<i>Chionoecetes opilio</i>	6.9	6.9	7.0	<0.1	94.0	7.7	1.4	0.1
<i>Ophiura sarsii</i>	6.9	13.8	22.5	0.5	50.8	7.7	8.4	2.1
<i>Psolus peronii</i>	5.2	19.0	6.0	41.1	26.9	51.9	4.3	24.7
<i>Echinarachnius parma</i>	3.9	22.9	33.0	0	11.9	0	52.4	0
<i>Ophiocten sericeum</i>	2.9	25.8	<0.1	11.1	6.0	80.8	0.1	4.3
<i>Similipecten greenlandicus</i>	2.5	28.3	0	7.3	0	78.9	0	2.9
<i>Argis</i> sp.	2.2	30.6	0.9	0.1	82.1	7.7	0.2	0.2
<i>Gorgonocephalus</i> sp.	2.2	32.8	2.8	<0.1	43.3	1.9	1.2	0.4
<i>Hyas coarctatus</i>	2.1	34.9	1.3	0.1	82.1	9.6	0.3	0.5
Number of taxa			247	246				
Total average biomass per station (g wet weight per 1000 m ²)			3849	16910				
Percent of total biomass			73.42	60.20				

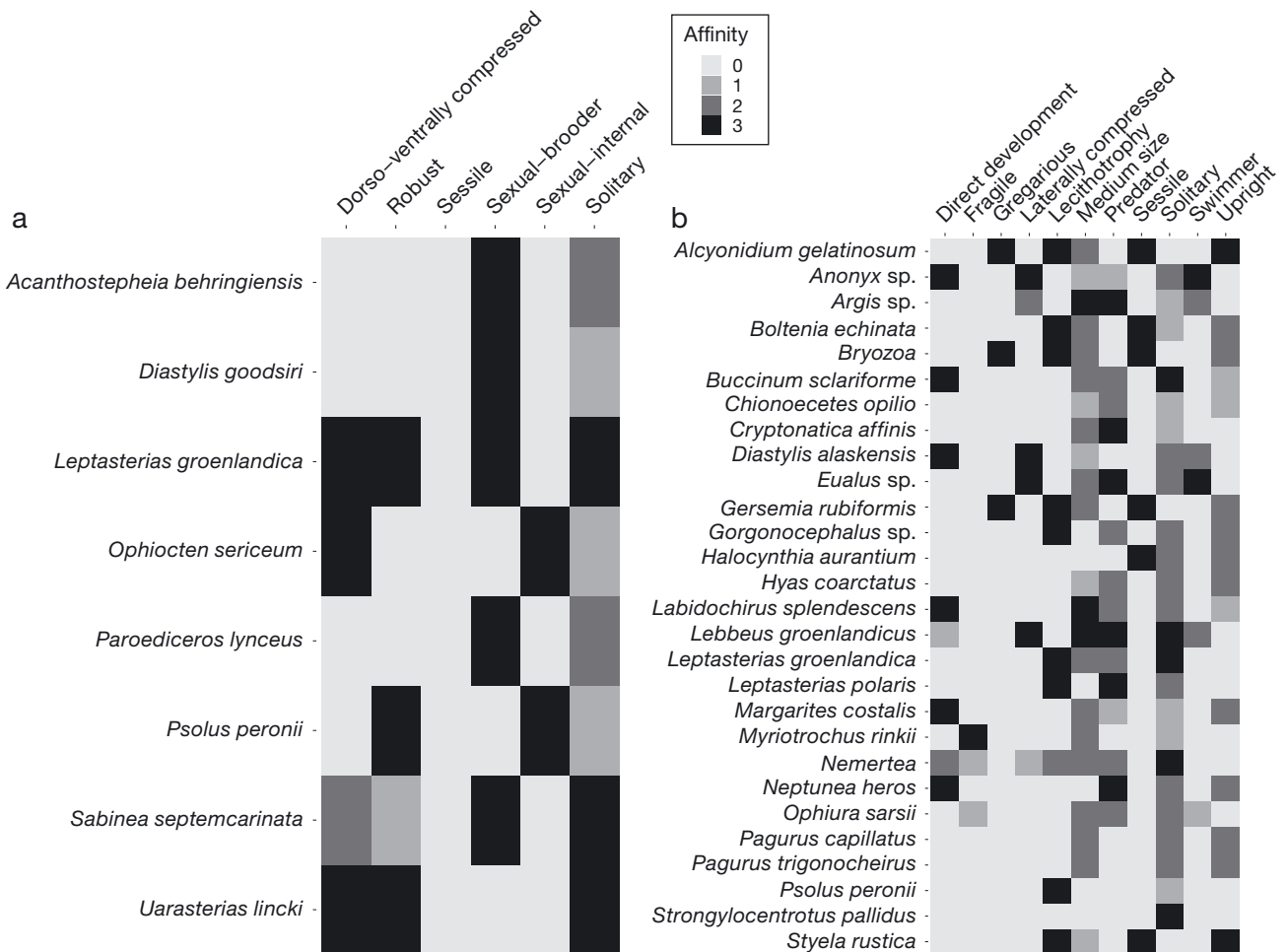


Fig. 7. Matrix of pairwise affinities between characteristic taxa and influential modalities in the (a) Beaufort Sea and (b) Chukchi Sea based on BVSTEP analyses with Spearman's correlation coefficient > 0.95 and p ≤ 0.001. Shading represents the affinity of a taxon for a given modality (from white = low affinity [0] to dark gray = high affinity [3])

plement to taxonomic diversity, especially on Arctic shelves (Rand et al. 2018), considering ecosystem function is likely to change with expected changes in taxonomic composition from climatic pressures (Renaud et al. 2015).

4.2. Functional diversity metrics

Epibenthic communities on both shelves were overall functionally similar, as indicated by comparable FRic and FDiv. However, we also observed differences in functional dissimilarity (Rao's Q) between the epibenthos of the 2 shelf systems, which were driven by significant differences in FEve. Differences in FEve were reflected in the more even distribution of modalities for the influential biological traits of body form, body size, and larval development in the Beaufort Sea compared with the Chukchi Sea community. Differences in biological trait expressions within a community will lead to differences in which resources are used within each community (McGill et al. 2006, Cadotte et al. 2011). Higher FEve and lower functional redundancy (although not significantly lower functional redundancy) in the Beaufort Sea community pointed to the use of a wider range of available resources within their respective niche space (Mason et al. 2005). For example, resource breadth for epibenthic shelf communities differs for substrate and food type. Sediments on the narrow Beaufort Sea shelf are a poorly sorted mix of gravel, sands, and muds, controlled by variable currents, river discharge, and ice rafting (Naidu 1974). In contrast, sediments on the broader Chukchi Sea shelf tend to be more uniform over larger regions in accordance with larger current systems (Grebmeier et al. 2015). Also, the Beaufort Sea shelf contains a diverse range of carbon sources as possible food sources for the benthos, including large amounts of terrestrial organic material from massive river discharge, marine phytoplankton, microphytobenthos, ice algal production, and macroalgal stands in the coastal Beaufort Sea (Bell et al. 2016, Harris et al. 2018). In contrast, there are fewer sources of macroalgae and terrestrial material on the Chukchi shelf. The higher FEve on the Beaufort shelf affords more opportunities to exploit such wider resource availability. Higher FEve also reflects a strong potential for maintenance of ecosystem function with loss of species due to a high degree of niche complementarity (Hewitt et al. 2008). Greater niche complementarity usually leads to greater resource partitioning within communities (Finke & Snyder 2008). In contrast, the

lower FEve in the Chukchi Sea community pointed to lower niche complementarity and, thus, a potential underutilization of resources (Mason et al. 2005). Higher functional redundancy in the Chukchi Sea could also lead to underutilization of resources, and is expected to increase with increasing temperatures through the borealization of the Chukchi Sea (Alabia et al. 2020). This scenario could lead to a system that is more vulnerable to invading species that would be able to capitalize on those available, underutilized resources (Tilman 2001). This is of particular importance to an inflow shelf such as the Chukchi Sea shelf, which receives species that are increasingly migrating northward from the Bering Sea in response to continued warming (Mueter & Lit-zow 2008, Stevenson & Lauth 2019, Thorson et al. 2019, Alabia et al. 2020).

4.3. Functional trait composition of Beaufort and Chukchi Sea epibenthos

4.3.1. Trait similarities between the shelves

Composition of functional traits on the Beaufort and Chukchi Sea shelves was similar in many aspects, as demonstrated through similar proportions of modalities within 5 biological traits. Shared trait composition should support similar ecosystem functioning (Lavelle & Garnier 2002). For example, benthic macrofaunal groups in the Baltic Sea clustered into groups based on shared biological trait composition that had similar effects on the ecosystem functions of stability and bioturbation (Villnäs et al. 2018, Liu et al. 2019). Similar modality composition between the Beaufort and Chukchi Sea shelves were seen in feeding habit, fragility, living habit, movement, and sociability. Many of these traits can be used to assess the vulnerability of benthic fauna to destructive forces and disturbances. Robustness of taxa, regeneration time, and position in the sediment have been used to assess benthic fauna vulnerable to disturbances such as the impact of predators (Weigel et al. 2016, Beauchard et al. 2017). Predator impacts may increase in Arctic shelf communities as ongoing and future habitat ranges of predatory species (e.g. Pacific and Atlantic cod) extend northward onto Arctic shelves (Rand & Logerwell 2011, Alabia et al. 2020). Such impacts could be further amplified if commercial fisheries were to move north into the Chukchi Sea from the Bering Sea, following demersal fish migrations (Christiansen et al. 2014). One could expect that the Beaufort and Chukchi Sea shelf systems would

respond in a similar way to those disturbances based on their similar composition of many functional traits.

Within the shared biological traits of feeding habit and movement, specifically, deposit feeding habit and crawling movement can have strong impacts on ecosystem services such as sediment oxygenation, resuspension, and remineralization through downward and horizontal movements of detrital particles (Snelgrove et al. 2000, Queirós et al. 2013). For example, brittle stars are a dominant taxon across the Beaufort and Chukchi Sea shelves (Ravelo et al. 2015, 2017, Iken et al. 2019), and the prominent species (*Ophiocten sericeum* and *Ophiura sarsii*, respectively) generally express a similar biological trait profile. They are mostly deposit feeders, have medium/robust fragility, free-living habits, burrowing and crawling movement types, and solitary life styles. These distinctive modalities in ophiuroids affect carbon and nutrient cycling in a similar way in both Arctic shelf systems through bioturbation (Kristensen 2000, Ambrose et al. 2001).

4.3.2. Trait differences between the shelves

Strong differences existed in modality composition in 4 biological traits between the Beaufort and Chukchi Sea shelves: larval development, reproductive strategy, body size, and body form. These traits, to varying degrees, have been observed to drive variation in benthic ecosystem function in the North Sea (Bolam & Eggleton 2014) and the Arctic Ocean (Degen 2015, Kokarev et al. 2017, Rand et al. 2018). We suggest that these traits also contribute to differences in ecosystem functioning between the Beaufort and Chukchi Sea shelf communities.

The Chukchi Sea community had a higher proportion of planktotrophic larval development compared to the Beaufort Sea community. Planktotrophic larval development and a sexual-external reproductive strategy provide epibenthic taxa with the ability to spread fast and far, which increases their ability to resist or recover after a disturbance (Węśławski et al. 2011). Planktotrophic larvae can spend days to months in the plankton phase because of their need to feed during development (Thorson 1950, Pechenik 1990, Buzhinskaja 2006). This planktonic duration is inversely correlated with temperatures, leading to typically longer times spent in the plankton for Arctic larvae (O'Connor et al. 2007, Ershova et al. 2019) due to reduced metabolic rates compared to regions with warmer water temperatures (Gillooly et al. 2002). For example, planktotrophic larval development time of

2 common crustaceans, the shrimp *Pandalus borealis* and the hermit crab *Pagurus bernhardus*, followed predicted exponential increases in larval duration with decreased temperature (O'Connor et al. 2007). Long larval development times, coupled with strong, large-scale advection driving a strong injection of larvae from the Bering Sea to the Chukchi Sea shelf (Ershova et al. 2019), allow Arctic taxa to efficiently colonize open space across large distances in the Chukchi Sea. In contrast, the Beaufort Sea shelf community, which does not possess a similar source of advected larvae, had high proportions of lecithotrophic and direct development. These development types either spend no time (direct development) or little time (lecithotrophic development) in the plankton, indicating a high level of preservation of local ecosystem processes mediated by these low-dispersal traits (Degen & Faulwetter 2019). These life history strategies may be an adaptation to the narrow Beaufort Sea shelf, likely reducing advective losses of larvae into unsuitable deep-sea habitats that could result from seasonally strong flow regimes (Pickart 2004). Also, direct or lecithotrophic development might be less affected by large-scale water column stressors. For example, high latitudes are particularly vulnerable to ocean acidification due to the naturally occurring low carbonate concentration derived from low water temperatures (Feely & Chen 1982, Byrne et al. 2010). These acidic conditions can be particularly detrimental to many of the pelagic early life stages of invertebrates (Long et al. 2013a,b). Brooding species with direct development are likely less affected by ocean acidification due to maternal protection of the developing juveniles compared with species with planktotrophic larval development that spend extended time periods in those conditions (Lucey et al. 2015).

Body size has been referred to as the master or key trait because it affects numerous aspects of ecosystem functioning because of its many relationships with other traits (Degen et al. 2018). For example, body size is highly correlated with behavioral traits such as predatory feeding habits (Riede et al. 2010, Nordström et al. 2015), where larger-sized predators typically consume larger-sized prey (Riede et al. 2010). Indeed, we found a higher proportion of typical upper trophic level feeding habits (i.e. scavengers and predators) in the larger-sized Chukchi epibenthos.

Body size can also influence nutrient cycling and energy turnover through metabolic rates (Hall et al. 2009). Nutrient cycling can be directly regulated by organisms, for example, through input of nitrogen to

a system via excretion and ingestion, and indirectly regulated through an organism's influence on microbial communities and primary production (Hall et al. 2009). In addition, communities with smaller-sized taxa (i.e. the Beaufort Sea community) will have a larger effect on energy turnover compared to those dominated by larger taxa, because smaller taxa have higher metabolic, excretion, and turnover rates (e.g. shorter generation time) (Pearson & Rosenberg 1978, Brown et al. 2004). Larger mobile marine invertebrates such as in the Chukchi Sea are more likely to travel greater distances, which would move energy in the form of biomass across the shelves on a large scale, similar to the large-scale effects of dispersive larvae on ecosystem function discussed in this section. Higher metabolic, excretion, and turnover rates of smaller mobile invertebrates, coupled with smaller dispersal potential in the Beaufort Sea community, may retain energy more locally compared to the Chukchi Sea community. This essentially creates a system where taxa in the Beaufort Sea are more restricted to use the local resources available, where high FEve reflects more efficient use of all available resources by the functionally more dissimilar assemblages (high Rao's Q).

Body form is often related to ecological roles such as bioturbation and habitat formation that can lead to ecosystem stability (Degen & Faulwetter 2019). Taxa with specific body forms can be vulnerable to common disturbances, which may destabilize ecosystem function (Jørgensen et al. 2015, 2019, Degen et al. 2018). For example, pressure from some predators or trawling will likely affect upright body forms more than vermiform or dorso-ventrally compressed body forms, because upright body forms have more above-ground exposure (Bremner et al. 2006, Jørgensen et al. 2019). Dorso-ventrally compressed body forms, in addition to vermiform body forms, increase bioturbation, which tends to foster ecosystem production and stability (Degen & Faulwetter 2019). Body form is more closely related to taxonomic identity than most other traits, i.e. biological traits are assigned to taxa that are typically identified based on morphological features (Beauchard et al. 2017). This close relationship between body form and taxonomy makes body form a contentious trait to include in functional diversity analyses (Beauchard et al. 2017). The inclusion of this trait has advantages and disadvantages due to the strong relationships that exist between body form-related traits and the taxa present in a region, which gives taxonomy disproportional weight in functional analyses. In our

study, we saw this relationship between dominant body forms and taxonomy in both shelf systems. For example, the Chukchi Sea epibenthos was mostly dominated by the dorso-ventrally compressed body form, which was reflected in the frequent and high biomass-contributing species such as *Chionoecetes opilio*, *Echinarachnius parma*, and *Ophiura sarsii*. In contrast, the Beaufort Sea epibenthos was dominated by globulose, dorso-ventrally compressed, and laterally compressed body forms, which were represented by the frequent biomass contributors *Psolus peronii*, *Ophiocten sericeum*, and *Similipecten greenlandicus*, respectively (note that *S. greenlandicus* and other bivalves were functionally coded as laterally compressed based on morphology, not necessarily reflecting their position on the seafloor). Although a tight relationship with taxonomy did exist, we considered the inclusion of body form necessary to glean information on community vulnerability to disturbances such as trawling. The Chukchi Sea shelf, which is directly north of the Bering Sea, will likely see increased commercial interest, but may be more resilient to this type of disturbance if the shelf remains dominated by taxa that are dorso-ventrally compressed.

5. CONCLUSIONS

The current benchmark of functional and taxonomic diversity metrics, and of functional and taxonomic composition, of Beaufort and Chukchi Sea epibenthic communities provided here will aid in future shelf-wide or among-shelf ecosystem function comparisons in the Alaskan Arctic. In the rapidly changing Arctic, these benchmarks will support interpretation of long-term monitoring data. Currently, differences in specific biological traits (e.g. body form, body size, larval development, reproductive strategy) lead to differences in ecosystem function between the Beaufort and Chukchi Sea epibenthic shelf communities. These differences mirror differences in taxonomic diversity, with the Beaufort Sea epibenthic community having significantly higher diversity. The combination of functional and taxonomic diversity metrics enables us to have a comprehensive understanding of how ecological niche space is currently used in Alaskan Arctic benthic shelf systems. Future studies should evaluate environmental influences on functional diversity, as well as on ecosystem function changes over time, and space so we can predict how the ecology of the Arctic benthos is likely to change.

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