

Isotopic and traits-based trophic diversity of Canadian Beaufort Sea benthic communities in relation to food supply

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Abstract

In the Arctic, climate-driven alterations to the quality and quantity of organic matter reaching the seafloor will likely affect benthic food web function. We used biomass-weighted diversity measures based on trophic traits (those related to feeding behaviours, e.g., mobility, size, food source), stable isotope ratios ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$), and taxonomy to assess linkages between benthic food web structure and indicators of food supply in the shelf and slope ecosystems of the Canadian Beaufort Sea and Amundsen Gulf (down to 500 m). Benthic communities across both regions used a similar diversity of sedimentary organic matter sources according to stable isotopes, despite known differences between regions in organic matter input and benthic–pelagic coupling. Shelf-edge and upper-slope communities exhibited relatively high trophic trait diversity, which likely reflected the exploitation of pulsed food inputs associated with dynamic processes at the shelf break that affect the production and advection of organic matter to the benthos. Pairwise relationships between trophic traits and sedimentary proxies of benthic food supply were not significant at the regional scale. However, cluster analyses supported the notion that trophic trait composition was influenced by proximity to the shelf edge, where food supply is influenced by episodic events that may not be reflected by in situ sedimentary proxies. Our findings add to growing evidence that evaluating trophic traits composition may provide more information regarding functional responses to changes in benthic food supply than either isotopic or taxonomic diversity indices alone.

Key words: trait–environment relationships, Beaufort Sea, Amundsen Gulf, RLQ, organic matter pathways

Résumé

Dans l'Arctique, les changements induits par le climat de la qualité et de la quantité de matière organique atteignant le plancher océanique affecteront probablement la fonction du réseau alimentaire benthique. Les auteurs ont utilisé des mesures de diversité pondérées par la biomasse basées sur des traits trophiques (ceux liés aux comportements alimentaires, par exemple, la mobilité, la taille, la source de nourriture), des rapports d'isotopes stables ($\delta^{15}\text{N}$ et $\delta^{13}\text{C}$) et la taxonomie pour évaluer les liens entre la structure du réseau alimentaire benthique et les indicateurs de l'approvisionnement alimentaire dans les écosystèmes du plateau et du talus de la mer de Beaufort canadienne et du golfe d'Amundsen (jusqu'à 500 m). Les communautés benthiques des deux régions utilisaient une diversité similaire de sources de matière organique sédimentaire selon les isotopes stables, malgré les différences connues entre les régions en matière d'apport de matière organique et de couplage benthique-pélagique. Les communautés du bord du plateau et du talus supérieur présentaient une diversité de traits trophiques relativement élevée, ce qui reflète probablement l'exploitation d'apports alimentaires pulsés associés à des processus dynamiques au niveau du rebord du plateau qui affectent la production et l'advection de matière organique vers le benthos. Les relations par paires entre les traits trophiques et les proxys sédimentaires de l'approvisionnement en nourriture benthique n'étaient pas significatives à l'échelle régionale. Cependant, les analyses en grappes appuyaient la notion que la composition des traits trophiques était influencée par la proximité du rebord du plateau continental, où l'approvisionnement

en nourriture est influencé par des événements épisodiques qui peuvent ne pas être reflétés par les proxys sédimentaires in situ. Ces résultats s'ajoutent aux preuves croissantes que l'évaluation de la composition des traits trophiques peut fournir plus d'informations sur les réponses fonctionnelles aux changements de l'approvisionnement en nourriture benthique que les indices de diversité isotopique ou taxonomique seuls. [Traduit par la Rédaction]

Mots-clés : relations traits–environnement, mer de Beaufort, golfe d'Amundsen, RLQ, voies de passage des matières organiques

Introduction

Benthic biodiversity and food web structure strongly influence ecological functioning of marine ecosystems (Snelgrove 1997; Snelgrove et al. 2018; Solan et al. 2020). Benthic communities affect carbon storage (e.g., Covich et al. 2004; Trueman et al. 2014), organic matter remineralization and nutrient cycling (Link et al. 2013a; Bourgeois et al. 2017), resilience to disturbance (e.g., Blanchard et al. 2011; Griffith et al. 2019), and the locations of feeding grounds for marine mammals (Bluhm and Gradinger 2008; L. Storrie, personal communication, 2021). In the Arctic, climate-driven changes to sea ice-ocean-atmosphere interactions are altering organic matter pathways that fuel benthic food webs (e.g., Hoegh-Guldberg and Bruno 2010; McLaughlin and Carmack 2010; Yurkowski et al. 2020). Effects on benthic food web functioning are expected to be spatially variable and influenced by factors that determine primary productivity and the availability of labile organic matter at the seafloor (Tremblay et al. 2011; Link et al. 2013b; Steiner et al. 2015; Tedesco et al. 2019).

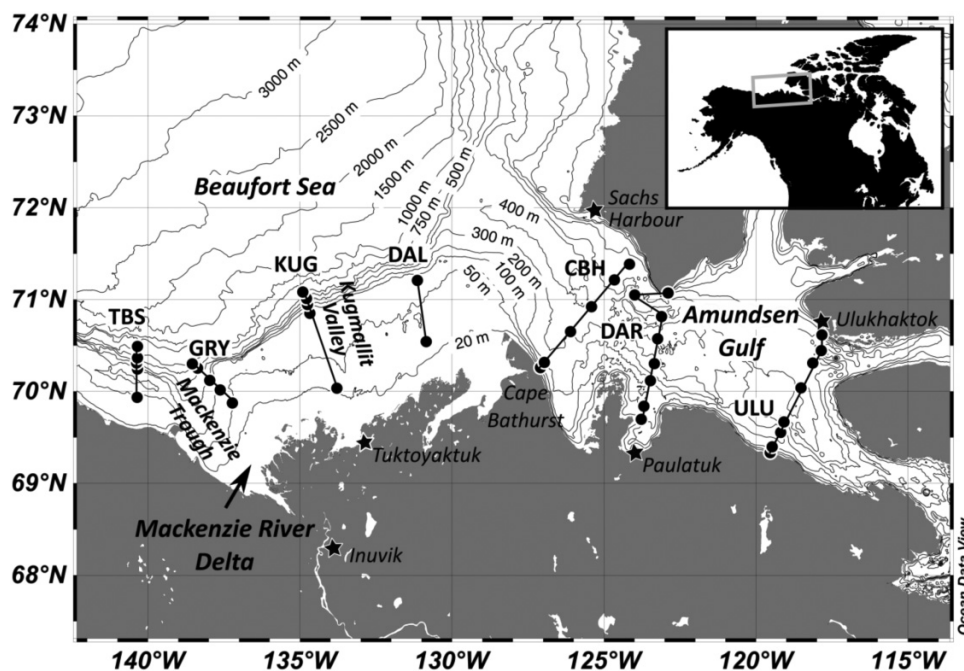
For marine benthic communities to be useful sentinels of shifting production regimes for Arctic conservation monitoring programmes (Solan et al. 2020), aspects of food web structure that vary with benthic food supply must be identified. To that end, biological traits analysis can describe ecological functioning via the abundance and distribution of species' traits that confer either a response to, or an effect on, ecological processes (Bremner et al. 2003). If ecosystem function is determined by traits of the most dominant species, as theorized (Grime 1998), the abundance and distribution of functional attributes will provide a more mechanistic understanding of community responses to environmental gradients than taxonomic measurements alone (Bremner et al. 2003; Mouillot et al. 2013). Indices of functional diversity and composition have thus emerged as potentially powerful ecological indicators for marine benthic communities (Beauchard et al. 2017) and are influenced by the quality and sources of organic matter available to benthos (e.g., Link et al. 2013b; Al-Hababeh et al. 2020; McGovern et al. 2020).

The variety of body forms in marine benthic communities precludes the use of easily measured quantitative traits that maintain a similar function across taxa. Consequently, recent biological trait analyses of Arctic marine benthic communities have relied on fixed, categorical traits that summarize important aspects of species functional roles (e.g., reproductive strategy, mobility; Degen and Faulwetter 2019; Liu et al. 2019; Włodarska-Kowalczyk et al. 2019; McGovern et al. 2020). From a trophic perspective, categorical traits that describe or affect feeding behaviours and food web interactions (e.g., predator, deposit feeder, mobility, body size) do not capture the inherent, and often substantial variation in

trophic ecology observed within species (e.g., Węśławski et al. 2010; Jumars et al. 2015). Stable isotope ratios ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) measured in the tissues of consumers can represent trophic breadth (Bearhop et al. 2004; Layman et al. 2007) and therefore fill the gap between the “fundamental” trophic diversity summarized by fixed traits and the “realized” trophic diversity expressed by a community. By treating $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ as quantitative trophic traits, isotopic diversity can be calculated using biomass-weighted methods akin to those used for functional and taxonomic diversity (Rigolet et al. 2015). Traits-based functional diversity often increases with taxonomic diversity due to the addition of new trait combinations (e.g., Liu et al. 2019), whereas isotopic diversity can function independently of taxonomic diversity because it is more closely linked to available organic matter sources (e.g., Włodarska-Kowalczyk et al. 2019). Functional food web structure can then be assessed from two sets of complementary information: (1) a set of fixed biological traits, which reflect the range of possible trophic functions a community can express (e.g., feeding modes, preferred food sources) and (2) a set of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values measured in consumers, which integrate dietary variation expressed across spatial and (or) environmental gradients

Here, we combined trophic diversity based on traits and stable isotope ratios to (i) describe spatial patterns in food web structure for benthic fish and epifaunal invertebrate communities across the Canadian Beaufort Sea and Amundsen Gulf; and (ii) investigate associations with gradients of sedimentary food supply and bottom oceanography. A lower sinking flux of pelagic organic matter (Sallon et al. 2011; Sampei et al. 2011) has been linked to weaker benthic–pelagic coupling and the use of a wider diversity of carbon sources among benthic consumers in the Amundsen Gulf relative to the Beaufort Sea (Stasko et al. 2018a). We predicted that (1) traits-based and isotopic trophic diversity would be greater in the Amundsen Gulf than in the Beaufort Sea; (2) higher taxonomic diversity would be positively related to traits based but not isotopic trophic diversity; and (3) the composition of trophic traits would be linked to gradients of organic matter delivery to the seafloor. Combining fish and benthic invertebrates provided a sufficiently large isotopic data set to explore the utility of combining traits-based and isotopic trophic diversity indices to identify important food web characteristics. Findings have relevance for monitoring local marine protected areas (MPAs), which aim to protect key habitats and food webs that support valued upper trophic marine mammals and seabirds (Tarium Nirvutait MPA and the Anguniqvia niqiyuam MPA; DFO 2013, 2014). Furthermore, this study provides regional context, as the MPAs encompass only a small portion of the benthic foraging habitat used by local marine mammal populations (e.g., Harwood et al. 2015; Stirling et al. 1977; L. Storrie, personal communication, 2021).

Fig. 1. Map of the Canadian Beaufort Sea and Amundsen Gulf region, showing the locations of sampling stations. Transects TBS, GRY, KUG, and DAL were sampled in 2012, whereas transects CBH, DAR, and ULU were sampled in 2013. Map produced using Ocean Data View ver. 5.4 (Schlitzer 2021).



Materials and methods

Study area

Sampling took place in the southern Canadian Beaufort Sea and Amundsen Gulf during the ice-free season from early August to mid-September of 2012 and 2013 (Fig. 1). The Beaufort continental shelf extends approximately 120 km offshore to the 200 m isobath, past which the seafloor descends steeply to several thousand metres. The Beaufort shelf is strongly influenced by freshwater and terrestrial sediment discharged from the Mackenzie River (Doxaran et al. 2015). The continental shelf in the Amundsen Gulf is much narrower, and maximum depths in the gulf are ~600 m. Primary production in the Amundsen Gulf generally exceeds that in the Beaufort Sea, but sinking export of pelagic production is lower, except in the vicinity of Cape Bathurst (Sallon et al. 2011; Sampei et al. 2011; Ardyna et al. 2013).

Collection of biological samples

Sampling occurred along seven transects that spanned the continental shelf and slope as part of the Beaufort Regional Environmental Assessment Marine Fishes Project (Fisheries and Oceans Canada; Fig. 1). The current study included 39 sampling stations with depths ranging from 20 to 500 m. Demersal fish and epifaunal invertebrates were quantitatively sampled from the commercial stern trawler F/V *Frosti* with a 3 m high-rise benthic beam trawl (6.3 mm mesh cod end liner; 4.27 m headrope and footrope). Trawling targeted a speed-over-ground of 2.0 knots (1.81–2.35 acceptable range) for 10 min bottom-contact time and was monitored with a Scanmar CGM-05/TE40-2 trawleye sensor (Scanmar, Åsgårdstrand,

Norway). Biota were sorted onboard to the lowest feasible taxonomic resolution. Where taxonomic doubt existed, specimens were frozen or preserved in a 10% formalin solution for subsequent verification by taxonomists from Université Laval and the Canadian Museum of Nature. Taxonomy was standardized to names currently accepted in the World Register of Marine Species (WoRMS Editorial Board 2020). The study and collection protocols were approved by the Fisheries and Oceans Canada Freshwater Institute Animal Care Committee and followed guidelines from the Canadian Council on Animal Care (<https://ccac.ca/en/standards/guidelines/>).

Collection of environmental data

Benthic community composition and food web structure in Arctic seas are influenced by large-scale environmental gradients which are defined by physical oceanographic conditions and by meso-scale environmental gradients that define sedimentary characteristics and benthic food supply (Link et al. 2013b, 2013a; Roy et al. 2014; Majewski et al. 2017; Yunda-Guarin et al. 2020). Eight habitat variables were therefore chosen to assess the influence of environment and benthic food supply on trait distributions (Table 1). Benthic Chlorophyll (Chl) *a* concentrations (mg m^{-2} of dry mass), sediment organic matter content (% of total dry mass), and the ratio of Chl *a*: phaeopigments (an indicator of the degradation of phytodetritus) were selected as proxies for the quality and quantity of energy available to benthic consumers (Link et al. 2013b; Roy et al. 2014). Stable isotope ratios of nitrogen ($\delta^{15}\text{N}$) measured in bulk sediments were used as an indication of the degree of microbially mediated transformation of sinking

Table 1. Mean, standard deviation (SD), maximum, and minimum values for oceanographic variables and sedimentary proxies for benthic food supply measured at 39 sites in the Canadian Beaufort Sea and Amundsen Gulf.

Environmental variable	Mean	SD	Max.	Min.
Bottom oxygen (mL L ⁻¹)	7.18	1.02	10.44	5.90
Bottom salinity (PSU)	33.34	1.40	34.86	29.43
Bottom temperature (°C)	-0.44	0.76	0.75	-1.43
Sediment Chl <i>a</i> (m ⁻²)	5.00	5.70	27.15	0.31
Sediment Chl <i>a</i> : phaeopigments	0.17	0.11	0.53	0.06
% Sediment organic matter	9.63	2.29	14.58	3.67
Sediment δ ¹⁵ N	4.83	1.81	7.74	-0.17
% Silt	70.37	17.17	90.34	0.20

particulate organic matter available at the seafloor, which increases with depth, but at different rates in the Beaufort Sea compared to the Amundsen Gulf (Kellogg et al. 2011; Stasko et al. 2018b). Stable isotope ratios of carbon (δ¹³C) were not available for many stations in the Amundsen Gulf, and thus they were excluded from the current analysis but would represent a useful indicator of the relative proportions of organic matter derived from different basal sources (fresh marine, refractory marine, and terrestrial) in future studies. Sediment grain size influences marine faunal distributions (e.g., Thrush et al. 2003; Cui et al. 2009). Sediments are predominantly muddy in the Beaufort Sea, so the slightly coarser proportion of sediment comprising of silt (%; 2–63 μm) was used as a meso-scale descriptor of sedimentary habitat because it captures more spatial variation in grain size than mud (0–63 μm). Bottom temperature (°C), salinity (practical salinity units, PSU), and oxygen concentrations (mL L⁻¹) were used as large-scale environmental variables, referred to collectively herein as bottom oceanography. The vertical water mass structure in the region results in strong collinearities between depth and bottom temperature, salinity, and oxygen concentrations (Lansard et al. 2012). Depth itself was therefore not included as the three bottom oceanography variables provide more information while concurrently acting as a proxy for depth. Bottom oxygen concentrations and temperature can influence fish and invertebrate distributions (e.g., Cui et al. 2009; Roy et al. 2014) as well as benthic biogeochemical cycles important to nutrient fluxes at the sediment interface (Link et al. 2013b).

Marine sediments were collected at each station with a 0.25 m² USNEL box core. The upper 1 cm of sediment was sampled for benthic organic matter content, pigment concentrations, and sediment δ¹⁵N and immediately frozen on-board at -50 °C. The upper 5 cm was sampled for granulometry and stored at 4 °C. Oceanographic profiles were taken at each station with a Seabird SBE-25 s/n 0415 (Sea-Bird Scientific, Bellevue, USA) conductivity, temperature, and depth probe and oxygen sensor mounted to a rosette equipped with 12 Niskin bottles for water sampling. Detailed methodologies for sedimentary analyses and oceanographic profiling are described in Niemi et al. (2020). Bottom oceanography variables were calculated using the three bottom-most profile measurements (no more than 15 m above the seafloor).

Stable isotope analysis

Stable isotope analyses on biological tissues and sediment were completed following the protocols described in Stasko et al. (2017) at the University of Waterloo Environmental Isotope Laboratory (Canada). The analytical precision for δ¹⁵N and δ¹³C was 0.3‰ and 0.2‰, respectively, based on repeated measurements of working laboratory standard material and NIST-1577b cross-calibrated to the international standards USGS-40, IAEA-CH6, -CH3, -N1 and -N2 (no less than 20% of each run). Repeatability of duplicate sample measurements (every 12th sample) was 0.3‰ for both δ¹⁵N and δ¹³C. Stable isotope data, summarized by species and location, are available in Stasko et al. (2017). δ¹³C for sediment and benthic invertebrates that could not be separated from exoskeletons were analysed from sub-samples acidified with 1 N HCl following Jacob et al. (2005).

Compilation of biomass and functional trait data

Biomass estimates were calculated from wet mass measured during field collections whenever possible and combined with wet mass measured in the laboratory from thawed fish and formalin-preserved invertebrates sent for taxonomic verification. Missing fish masses for damaged specimens were estimated from species-specific regressions of total length on mass for conspecifics caught during sampling, where possible. Estimated masses were used for 4.1% of individuals; 1.5% was removed due to a lack of reliable length measurements. Biomass was standardized to catch-per-unit-effort at each site by calculating density (g m⁻²) using the total swept area (see Niemi et al. 2020).

Prior to statistical analyses, taxa that never consisted of more than 1% of the total biomass at any sampling station were removed from analyses to reduce biases created by rare species and to improve the detection of underlying community patterns by multivariate analyses (Clarke and Warwick 2001). Constraining the taxa list in this way removed most instances of taxa that occurred only at a single site (18 singletons remained). Planktonic species likely caught during net retrieval were also removed. A total of 106 taxa representing 62 families and 12 phyla were retained for final analyses (Supplementary Material 1).

Five functional traits relevant to trophic ecology were subdivided into 25 trait modalities and used to represent trophic

Table 2. Descriptions of functional traits and trait modalities selected for analysis.

Trait	Modality	Code	Description
Mobility	Sessile	M.sess	Generally does not move; may be attached.
	Discretely mobile	M.dismob	Capable of free movement but does not actively move to feed (e.g., sea anemones)
	Crawler	M.crawler	Crawls freely on the sediment surface
	Swimmer	M.swimmer	Not restricted to movement directly on the seafloor; water-associated.
	Burrower	M.burrower	Capable of free movement but dwells in burrows in the sediment
	Tubicolous	M.tubicolous	Tube dwelling; restricted movement
Feeding type	Suspension feeder	FT.susp	Feeds on fresh or resuspended particulate organic matter (no restriction on particle size)
	Deposit feeder	FT.dep	Feeds on material deposited on the sediment surface including, but not limited to, large food falls, detritus, carcasses, and fecal pellets from the overlying water column, bacteria, and bacterial products
	Predator	FT.pred	Feeds by actively capturing live animal prey
	Scavenger	FT.scav	Feeds on dead animal material
Body size	20 mm	BS.20	Maximum recorded body size ≤ 200 mm
	100 mm	BS.100	Maximum recorded body size ≤ 100 mm
	250 mm	BS.250	Maximum recorded body size ≤ 250 mm
	500 mm	BS.500	Maximum recorded body size ≤ 500 mm
	750 mm	BS.750	Maximum recorded body size ≤ 750 mm
	12 000 mm	BS.1200	Maximum recorded body size ≤ 1200 mm
Particle transport	Resuspension	PT.resusp	Actions of the organism resuspend particulate matter
	Sediment mixing	PT.mix	Actions of the organism mix the sediment; no restriction on depth of mixing
	advection	PT.adv	Actions of the organism advect particulate matter across relatively long distances, either horizontally or vertically (e.g., fish migrations move particulate matter through excretion)
Food source	POM	FS.pom	Feeds on particulate organic matter (POM)
	Detritus	FS.det	Feeds on detritus at the sediment surface
	Microfauna	FS.mic	Feeds on microfauna (e.g., diatoms, bacteria, and other single-celled organisms)
	Macrofauna	FS.mac	Feeds on macrofauna
	Phytoplankton	FS.phy	Feeds on phytoplankton that has settled to the seafloor
	Zooplankton	FS.zoo	Feeds on zooplankton

Note: Trait choices follow those described by [Macdonald et al. \(2010\)](#) and the Arctic Traits Database with some minor modifications to account for trait collinearity. Codes are used to represent traits in figures.

functionality (Table 2). Selected traits either directly influence how a species obtains food (e.g., feeding mechanisms) or indirectly influence food web structure and function (e.g., particle transport and body size). Many of the selected traits and modalities demonstrably reflect the ecological functioning and trophic interactions of benthic marine communities ([Bremner et al. 2006](#); [Cirtwill and Eklöf 2018](#); [Laigle et al. 2018](#); [McGovern et al. 2020](#)). Redundancy and correlation among traits were avoided by assessing correlation matrices of community-weighted means of trait values ([Garnier et al. 2004](#)). Traits and trait modalities followed [Macdonald et al. \(2010\)](#) and the Arctic Traits Database, with some modifications to capture multiple traits that had strong collinearity. Information used to assign trophic trait modalities was derived from the primary literature, grey literature, and online databases including the Arctic Traits Database ([Degen and Faulwetter 2019](#); see Supplementary Material 2). A fuzzy coding approach ([Chevenet et al. 1994](#)) was used to assign the affinities of taxa to each trait modality, between 0 (no affinity) and 1 (high affinity). Fuzzy coding captures trophic flexibility by allowing taxa to be assigned an affinity >0 for multiple trait modalities. Affinity scores for modalities were

standardized to sum to 1 within each trait to give the same weight to each taxon and each trophic trait. When a taxon could not be assigned an affinity due to missing information, it took the mean trait profile for all other taxa to avoid influencing subsequent trait analyses ([Statzner and Bêche 2010](#)). Fuzzy-coded affinity scores and references for all taxa can be found in the Supplementary Material.

Spatial variability and associations between traits-based, isotopic, and taxonomic diversity

Taxonomic diversity at each sampling station was quantified with taxonomic distinctness (the average phylogenetic path length between randomly selected individuals; [Warwick and Clarke 1995](#)), Pielou's evenness (J'), and absolute species richness (number of species observed at each station). Traits-based trophic diversity was quantified at each station using the metrics functional dispersion (FDIs), functional evenness (FEve), and functional richness (FRic; ([Villéger et al. 2008](#); [Laliberté and Legendre 2010](#)). FDIs is calculated as the mean distance of taxa to the community centroid in multivariate trait space with taxa weighted by their relative biomass

densities (Laliberté and Legendre 2010). FDis is therefore conceptually and computationally similar to the centroid distance (CD) metric commonly used to describe isotopic niche space in food web studies (Layman et al. 2007) and was selected as an appropriate analogue for comparison with isotopic dispersion (see below). FDis, FEve, and FRic were computed for each sampling station using the package “FD” (Laliberté et al. 2014) from a table of taxa biomass densities and a multi-trait dissimilarity matrix of fuzzy-coded traits computed using the “gawdis” function to account for non-independence of trait modality blocks (de Bello et al. 2021). Biomass densities were square root of transformed prior to calculations of traits-based diversity metrics to decrease the influence of rare and overly dominant taxa (Clarke and Warwick 2001). Isotopic dispersion (IDis; Rigolet et al. 2015) was calculated for each sampling station using the same method as FDis, but with the means and standard deviations of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for each taxon at each station treated as “traits”. Because IDis is a relative measurement, there is no need to adjust $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ to account for spatial variation in isotopic baselines (Post 2002). IDis was only calculated for sampling stations where $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were available for taxa that consisted of at least 70% of the total biomass of the community (range of 70.8%–91.2% at 24 of 39 stations; Rigolet et al. 2015).

Analysis of covariance (ANCOVA) was used to test for differences in traits-based and isotopic trophic diversity metrics between the Beaufort Sea and Amundsen Gulf (prediction 1). Complementary taxonomic diversity metrics were treated as covariates in ANCOVA models: (1) taxonomic distinctness was the covariate in regional comparisons of FDis and IDis because all three metrics are independent of species richness (Warwick and Clarke 1995; Laliberté and Legendre 2010); (2) Pielou’s evenness was the covariate in the regional comparison of FEve; and (3) absolute species richness was the covariate in the regional comparison of FRic. Post hoc linear regressions were used to further evaluate the significance of relationships between traits-based, isotopic, and taxonomic trophic diversity metrics (prediction 2). Linear regressions were performed separately for the Beaufort Sea and Amundsen Gulf in cases where there was a significant interaction between the region and the covariate. ANCOVA results are reported using type III errors. Model assumptions were evaluated with histograms of residuals (normality of residual errors), Levene’s test (equal variances), and using the “gvlma” package in R (heteroscedasticity).

Spatial patterns in diversity indices were visualized with heatmaps. All maps were produced using the open-source software Ocean Data View ver. 5.4 (Schlitzer 2021) and its associated base maps.

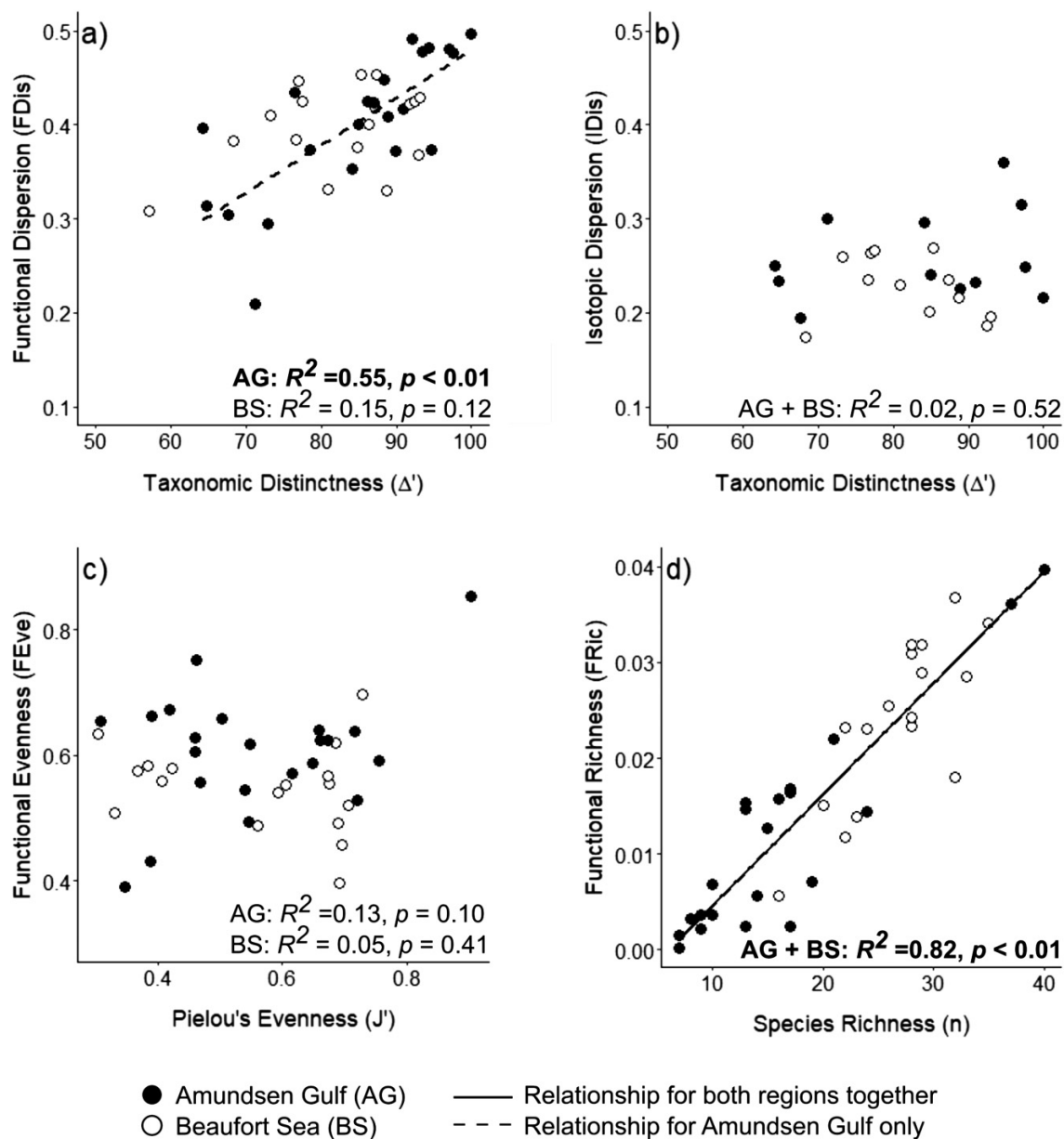
Testing trait-environment linkages

The combined RLQ and fourth-corner method (Dray et al. 2014) was used to assess whether trophic trait composition was linked to environmental gradients that reflected organic matter delivery to the seafloor (prediction 3). Both RLQ and fourth-corner analysis simultaneously analyse the information contained in three tables: table R contains a set of environmental variables for each sampling site, table L

contains abundances or biomass measurements for each taxon by station, and table Q contains information for a set of functional traits measured in each taxon (in this case, a table of fuzzy-coded ordinal variables). RLQ analysis finds linear combinations of traits and environmental variables that maximize their squared cross-covariance and provides a graphical summary of the joint structure among the three tables via multivariate ordination (Dolédec and Chessel 1994; Dolédec et al. 1996). However, RLQ does not provide a method for testing trait-environment relationships. Fourth-corner analysis tests the statistical significance of bivariate associations between each possible pair of traits and environmental variables but does not consider covariation among traits or environmental variables (Legendre et al. 1997). We used the methods jointly to explicitly test how organism traits respond to environmental gradients, using the package “ade4” in R (Dray and Dufour 2007). Briefly, RLQ analysis was first used to test the significance of the overall link between traits and environmental variables, mediated through the distribution of taxa biomasses across stations (via correspondence analysis of the square-root transformed table L, principal components analysis of table R, and fuzzy correspondence analysis of table Q wherein traits were column-weighted by trait modality blocks; see detailed methodology in Kleyer et al. (2012) and Dray et al. (2014). The resultant multivariate ordination scores for environmental variables (sites) and taxa traits (species) were then used in fourth-corner analysis to evaluate the statistical significance of their relationships to the original trait and environmental variable data. To test for significant relationships between all possible pairwise combinations of traits and environmental variables, a second fourth-corner analysis was conducted using original trait and environmental data. The global significance of the RLQ analysis was evaluated using the S_{RLQ} statistic (Dray and Legendre 2008). Bivariate fourth-corner relationships were evaluated using square correlation coefficients (Dray et al. 2014). In both cases, test statistics were generated by sequential random permutations of sites and species using Model 6, which combines Model 2 (null hypothesis that table R is not related to table L) and Model 4 (null hypothesis that table L is not related to table Q) (Dray and Legendre 2008). Inflated type I error rates associated with multiple testing were accounted for by using a high number of permutations (99 999) and by using the false discovery rate method to adjust p values (Benjamini and Hochberg 1995). Environmental variables were $\log(x + 1)$ transformed where necessary to improve normality (dissolved oxygen, Chl a : phaeopigments ratio, and sediment Chl a). Four stations were removed from analyses because of missing (TBS_04, KUG_05) or outlying (DAR_01, DAL_02, % silt) environmental data.

To visualize the distribution of trophic traits among stations, and potentially identify environmental gradients not included in the RLQ-fourth corner analysis, functional composition at each station was summarized with community weighted means of trait values, wherein the trait modalities present in a community were weighted by the relative biomass densities of the species that exhibit them (Garnier et al. 2004). Hierarchical clustering using group-average linking was performed on a Bray–Curtis dissimilarity matrix of

Fig. 2. Relationships between traits-based and taxonomic diversity indices, including (a) traits-based trophic functional dispersion (FDis) and taxonomic distinctness (Δ'), (b) isotopic functional dispersion (IDis) and taxonomic distinctness, (c) traits-based functional evenness (FEve) and Pielou's evenness, and (d) traits-based functional richness (FRic) and species richness. Regression coefficients (R^2) and p values are from linear regression analyses, performed separately for the Amundsen Gulf (AG) and Beaufort Sea (BS) in cases where ANCOVA revealed a significant difference between regions. Values in bold indicate significant relationships. Traits-based diversity was significantly, positively related to taxonomic richness (both regions combined), and to taxonomic distinctness (AG only), whereas IDis and taxonomic distinctness were not related. Contrary to predictions, traits-based diversity did not differ between regions for most metrics except FDis.



community weighted means of trait values to identify sampling stations that had similar functional composition. The trait modalities “M.tubicolous” and “M.sessile” were very rare and removed prior to clustering analysis. Significant clusters were identified using approximately unbiased probability values calculated via multiscale bootstrap resampling with 99 999 iterations using the R package “pvclust” (Suzuki et al. 2019). Non-metric multidimensional scaling of the Bray–Curtis dissimilarity matrix was then used to visualize the

rank-order dissimilarities among stations in relation to trait modalities and to verify groupings identified by hierarchical clustering, using the R package “vegan” (Oksanen et al. 2020). The number of dimensions to retain is 6. Non-metric multidimensional scaling (NMDS) ordination was evaluated with stress, wherein stress <0.1 indicated good interpretability with two dimensions (Clarke and Warwick 2001).

Indicator values (IndVal) were calculated from the community-weighted mean trait values to find the trophic

Table 3. Results of linear regression analyses between pairwise combinations of traits-based trophic diversity indices (FDis, FEve, and FRic) with analogous taxonomic diversity indices (taxonomic distinctness, Pielou's evenness, and species richness), as well as linear regressions between isotopic trophic diversity (IDis) and taxonomic distinctness. Linear regressions were performed separately for the Amundsen Gulf and Beaufort Sea when ANCOVA analyses indicated a significant effect of the region on the relationship. Only sites where stable isotope data were available for taxa representing >70% of cumulative biomass were included in regressions with IDis. Significant relationships ($p \leq 0.05$) are in bold. All significant relationships were positive.

Test	<i>n</i>	<i>df</i>	<i>F</i>	<i>R</i> ²	<i>p</i>
FDis vs. taxonomic distinctness					
Amundsen Gulf	22	1, 20	24.89	0.55	<0.01
Beaufort Sea	17	1, 15	2.73	0.15	0.12
IDis vs. taxonomic distinctness	24	1, 22	0.44	0.02	0.52
FEve vs. Pielou's evenness					
Amundsen Gulf	22	1, 20	2.93	0.13	0.10
Beaufort Sea	17	1, 15	0.73	0.05	0.41
FRic vs. species richness	39	1, 37	172	0.82	<0.01

trait modalities that were most strongly associated with each station cluster (Dufrêne and Legendre 1997). An IndVal index of 100% indicates a trait modality that is observed at all stations of one cluster and not in any other cluster. Significant IndVal indices were determined using 9999 random permutations of stations using the "labdsv" package in R (Roberts 2019).

Fish and benthic invertebrate communities were analysed together in all analyses. The Beaufort Sea and Amundsen Gulf were analysed as one system for all tests of trait-environment linkages. All statistical and graphical procedures were performed in R ver. 4.0.4 (R Core Team 2021). Parametric tests were considered significant at $p < 0.05$. Bootstrapped tests were considered significant if the probability of obtaining the test statistic was <0.05 based on permuted data.

Results

Spatial variability and associations between traits-based, isotopic, and taxonomic diversity

Regional differences between traits-based trophic diversity metrics varied by metric (Fig. 2), as did relationships between traits-based trophic diversity and taxonomic diversity (Table 3). Values of functional dispersion (FDis) ranged from 0.21 to 0.50 (Fig. 3a). FDis was significantly different between the Amundsen Gulf and Beaufort Sea (ANCOVA, $F_{[1,35]} = 4.74$, $p = 0.04$), but the difference was dependent on taxonomic distinctness (significant interaction between region and the covariate; ANCOVA, $F_{[1,35]} = 4.66$, $p = 0.04$). Post hoc linear regressions revealed that FDis was significantly, positively related to taxonomic distinctness in the Amundsen Gulf only (Table 3). Relatively high FDis values occurred along the shelf break of the Beaufort Sea and along the northern margins of the Amundsen Gulf, near steep bathymetry (Fig. 3a). Values of FEve ranged from 0.39 to 0.85 (Fig. 3c). FEve was marginally significantly higher in the Amundsen Gulf compared to the Beaufort Sea (ANCOVA, $F_{[1,35]} = 4.20$, $p = 0.05$), but the relationship between FEve and Pielou's evenness was not

significant in either region (Table 3, Fig. 2c). Values of FRic ranged from <0.01 to 0.04 (Fig. 3d). FRic was not significantly different between the Beaufort Sea and Amundsen Gulf (ANCOVA, $F_{[1,36]} = 0.72$, $p = 0.41$) and was significantly, positively related to species richness (Table 3, Fig. 2d).

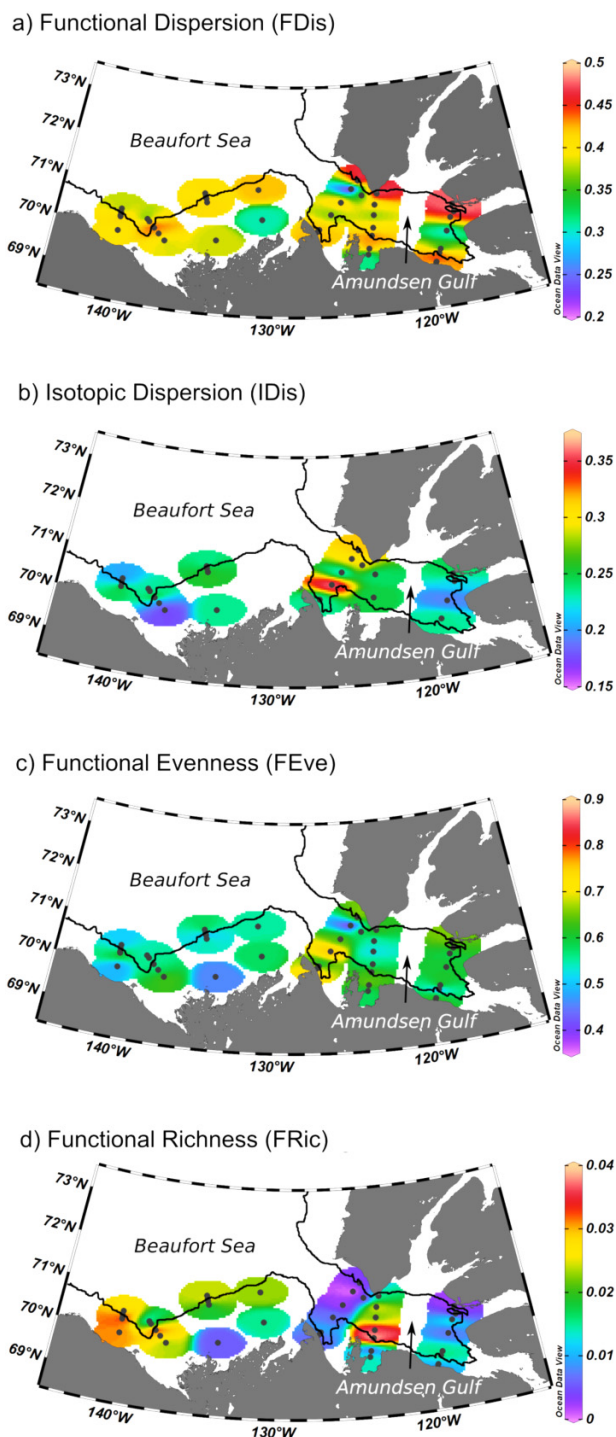
Values of IDis ranged from 0.17 to 0.48 (Fig. 3b) and, contrary to predictions, were not significantly higher in the Amundsen Gulf compared to the Beaufort Sea (ANCOVA, $F_{[1,21]} = 4.3.28$, $p = 0.08$). Consistent with our prediction, isotopic trophic dispersion (IDis) was not related to taxonomic distinctness (Table 3, Fig. 2b).

Testing trait-environment linkages

The overall joint structure between traits and environmental variables was significant ($S_{RLQ} = 2.22$, $p = 0.03$; Model 2, $p = 0.02$; Model 4, $p = 0.04$), with the first and second RLQ axes accounting for 84.12% and 7.10% of cross-covariance, respectively. Fourth-corner analysis indicated that environmental gradients on the first RLQ axis (represented by site scores) were significantly positively related to trait modalities associated with obligatorily benthic species, including discrete mobility, crawling, body size ≤ 20 mm, and activity that re-suspends particulate matter. Environmental gradients were significantly negatively related to the swimming and advection of particulate matter, which are generally associated with fish and large decapods (Fig. 4a). Overall, the variation in trait structure (species scores on the first RLQ axis) was significantly positively related to bottom oxygen concentrations and significantly negatively related to bottom temperature, indicating a depth gradient (lower temperatures and higher oxygen concentrations in shallow relative to deep habitats; Fig. 4b). However, the fourth-corner analysis revealed no significant relationships between specific pairwise combinations of trait modalities and proxies of benthic food supply (data not shown).

Three significant station clusters were identified by hierarchical cluster analysis of community-weighted mean trait values and named for their distinctive characteristics (Fig. 5a). The first group, named the hyperbenthic community cluster,

Fig. 3. Maps showing regional values for (a) functional dispersion (FDIs), (b) isotopic dispersion (IDIs), (c) functional evenness (FEve), and (d) functional richness (FRic) with the shelf break at 200 m outlined in black. IDIs is only displayed for sampling stations where stable isotope data were available for taxa that consisted of $\geq 70\%$ of the total biomass of the community. FDis and FEve were significantly different between the Beaufort Sea and Amundsen Gulf, whereas IDIs and FRic were not. FDis values highlighted a relatively high diversity of traits within communities located near shelf break that was not similarly evident in IDIs values. Maps were produced using Ocean Data View ver. 5.4 (Schlitzer 2021) and associated base maps.



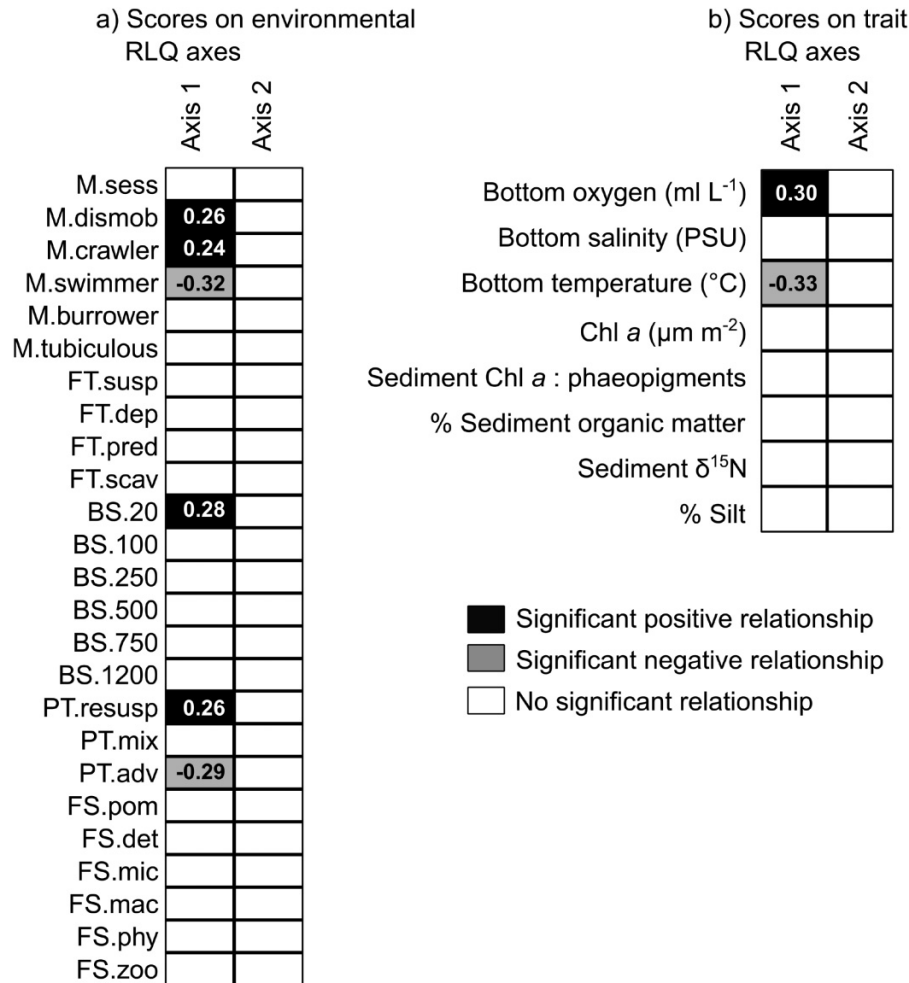
was characterized by trophic trait modalities that included predatory feeding modes, swimming, advective particle transport, and feeding on zooplankton (Table 4). Hyperbenthic communities were generally located on the upper continental slope (275–350 m depths) of the Canadian Beaufort Sea and Amundsen Gulf (Fig. 5b). The second, deposit-feeding dominated cluster included stations that were proximate to especially steep bathymetric features. This second cluster was characterized by trophic trait modalities that included deposit feeding, maximum body sizes ≤ 100 mm, and bioturbation of sediment (Table 4). The third and most distinctive cluster (IndVal indices > 0.6) was named the Amundsen Gulf shelf break cluster for its consistent station locations within a narrow depth range corresponding to the shelf break in the Amundsen Gulf (75–200 m depths; Fig. 5b). The Amundsen Gulf shelf-break cluster was characterized by trophic trait modalities that included discrete mobility, suspension-feeding, feeding on POM, and sediment resuspension. NMDS ordination agreed well with station clustering, and with the associations between station clusters and trophic trait modalities (Fig. 6).

Discussion

We investigated relationships between the trophic diversity of fish and epifaunal invertebrate communities and indices of benthic food supply and large-scale oceanography in two contiguous, but environmentally heterogeneous Arctic shelf ecosystems. Comparisons between traits-based and isotopic trophic diversity provided insight regarding spatial variation in potential and realized trophic structure, but did not reveal the strong differences expected between the Canadian Beaufort Sea and Amundsen Gulf. The distribution of trophic traits varied with bottom oceanography in a way that suggested an influence of depth, or possibly of summer ice clearance from the shelf (Yunda-Guarin et al. 2020), but did not vary significantly with the proxies for benthic food supply measured in this analysis. Instead, several lines of evidence, including the clustering of stations based on community-weighted trait compositions, suggested that communities near shelf-break habitats in both regions were influenced by organic matter delivery pathways that distinguished them from communities on the shallow shelf or deeper Amundsen Gulf. We suggest that trophic trait composition appeared to be influenced by local-scale, dynamic habitat filters that affected benthic food supply, but those habitat filters were neither well represented by benthic environmental variables measured at regional scales nor reflected in biomass-weighted stable isotope indices.

Traits-based and isotopic trophic diversity highlighted different regional patterns in food web structure, suggesting that each method provided distinct and complementary information. Trophic trait dispersion (FDIs) was highest in communities located near the continental shelf break and upper slope in both the Beaufort Sea and Amundsen Gulf. Upper continental slopes contribute disproportionately to ecosystem functioning relative to their habitat area on a pan-Arctic scale (Bluhm et al. 2020). Frequent but episodic hydrographic

Fig. 4. Combination of the RLQ and fourth-corner results, displaying relationships between (a) the overall structure of environmental gradients (represented by site scores on RLQ axes) and specific trophic functional traits and (b) between the overall structure of traits (represented by species scores on RLQ axes) and specific environmental variables. Numbers in boxes represent square correlation coefficients measuring linkages between variables in the fourth-corner analysis. Codes for traits are defined in Table 1. The overall structure of traits was significantly related to bottom oxygen and temperature, reflecting a separation of traits associated with obligate benthic species in shallower habitats from traits associated with hyperbenthic species in deeper habitats, where there are higher temperatures and lower oxygen concentrations.

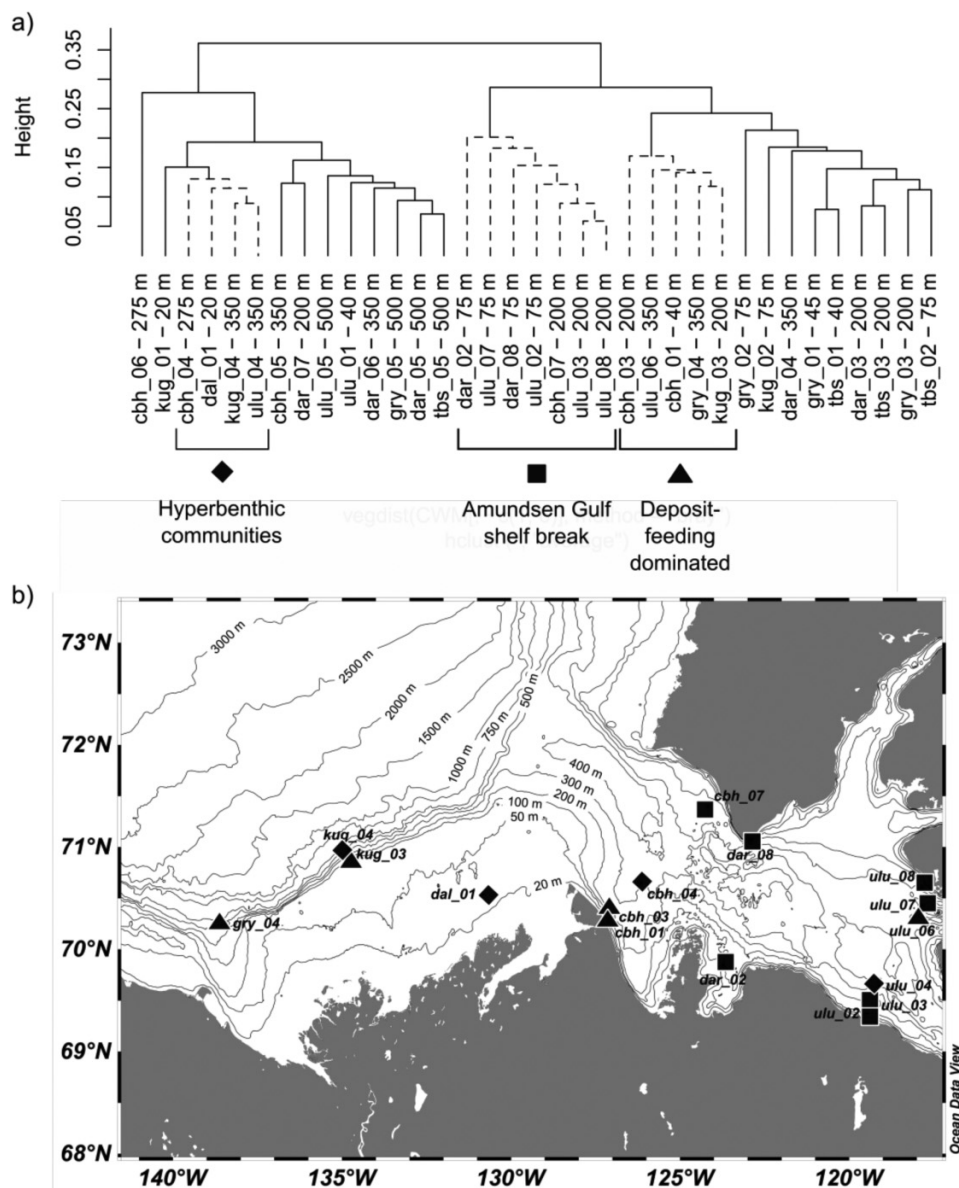


events at continental shelf edges are known to affect production regimes by facilitating the exchange of nutrients and biogenic material (Springer et al. 1996; Carroll et al. 2008; Bluhm et al. 2020; Randelhoff et al. 2020). Nutrient delivery from shelf-break exchange is particularly important for new primary production across the pan-Arctic interior shelves, and upwelling-favourable winds dominate in the Beaufort Sea (Williams and Carmack 2015; Randelhoff et al. 2020). Moreover, wind forcing produces a bottom-intensified shelf-break jet at approximately 150 m depths that is characterized by high and temporally variable current velocities, seasonal flow reversals, and eddy formation, all of which enhance the transport and re-suspension of particulate matter along and across the shelf break (Nikolopoulos et al. 2009; O'Brien et al. 2011; Forest et al. 2015). We propose that high trophic trait dispersion at shelf-edge and upper-slope habitats facilitates the

capture of pulsed food inputs by providing a variety of means for sequestering the energy (e.g., capture of different particle sizes, use of fractions that have undergone varying degrees of bacterial processing).

In contrast to functional diversity, isotopic diversity (IDis) exhibited relatively low spatial variability. Although polar benthic communities respond quickly and opportunistically to freshly sedimented or advected organic matter, the majority of their nutrition is derived from longer-term sedimentary stores (Mincks et al. 2005; Renaud et al. 2008). Consequently, benthic biomass and consumer stable isotope values in polar seas tend to reflect long-term indicators of benthic food supply rather than seasonal or episodic food inputs (Renaud et al. 2008; Kędra et al. 2012). If benthos relied primarily on sedimentary organic matter, spatial variation in δ¹⁵N and δ¹³C of benthic invertebrates and the fish

Fig. 5. (a) Dendrogram of station clusters resulting from a hierarchical clustering of community-weighted mean trait values and (b) the locations of clustered stations. Amundsen Gulf shelf break communities were located in a narrow depth range (72–200 m) on the hydrographically dynamic continental shelf edge surrounding the Amundsen Gulf, and deposit-feeding dominated stations were mostly located near areas with topographically enhanced upwelling. Habitat features that linked stations in the hyperbenthic communities cluster were less apparent.



that prey on them would be expected to reflect prominent organic matter sources, regardless of whether communities possess trophic traits to capture episodic food inputs (see further discussion below). The only exception in this study was an isotopic diversity “hotspot” near Cape Bathurst, which is likely linked to frequent upwelling that can cause high deposition of organic matter to the benthos in summer (Williams and Carmack 2008; Sampei et al. 2011; Darnis et al. 2012), similar to other Arctic hotspots with tight benthic–pelagic coupling (e.g., Chuckchi Shelf, Grebmeier et al. 1989; Barents Sea marginal ice zone, Tamelander et al. 2006; North Water Polynya, Olivier et al. 2020). Most polar benthic communities, however, likely exhibit limited temporal fluctuation in

stable isotopic values even if they consume pulsed food inputs (Kedra et al. 2012).

The clustering of Amundsen Gulf shelf-break communities supports the notion that episodic organic matter pathways contribute to structuring benthic trait composition. Station locations in this cluster were coincident with distinct taxonomic composition relative to other areas in the Canadian Arctic Archipelago (Roy et al. 2014), had some of the highest FDis values of all stations, and were defined by trophic trait modalities that suggested suspended particulate organic matter was a dominant basal resource. Similarly, most stations within the deposit-feeding dominated cluster occurred near the upper slopes at Cape Bathurst, Kugmallit Valley, or

Table 4. Significant indicator trait modalities associated with each station cluster were identified by hierarchical cluster analysis of community-weighted mean trait values across the Beaufort Sea and Amundsen Gulf. An IndVal index of 100% indicates a trait modality that is observed at all stations of one cluster and not in any other cluster. Station depth for each cluster is presented as a mean and range (max, min).

Station cluster	N sites	Significant indicator traits	IndVal (%)	<i>p</i>	Station depth (m)
Hyperbenthic communities	4	Food Source—zooplankton	43.33	0.001	249 (350, 20)
		Mobility—swimmer	37.51	0.004	
		Particle transport—advection	37.47	0.008	
		Feeding type—predator	35.76	0.001	
Deposit-feeding dominated	5	Feeding type—deposit feeder	34.86	0.026	228 (350, 40)
		Body size – 100 mm	32.51	0.045	
		Particle transport—sediment mixing	31.43	0.043	
Amundsen Gulf shelf-break	7	Mobility—discretely mobile	66.14	0.001	129 (200, 75)
		Food source—POM	64.71	0.001	
		Feeding type—suspension feeder	56.34	0.001	
		Particle transport—resuspension	39.70	0.006	

Mackenzie Trough. Bathymetric features at these locations, as well as at other submarine canyons that intersect Arctic shelves, are known to enhance the upwelling of nutrient-rich waters (Carmack and Kulikov 1998; Williams and Carmack 2008, 2015; Williams et al. 2008). A large proportion of the resultant new primary production sinks ungrazed to the benthos (e.g., Sampei et al. 2011), where it can promote high benthic biomass and a dominance of deposit feeders (Conlan et al. 2013; Link et al. 2013b).

Stations in the hyperbenthic cluster were not linked by any obvious habitat features, and unlike the other two clusters, were dominated by hyperbenthic fish and decapods (>84% relative biomass; Supplementary Material 3). This result was likely a consequence of the unique trait compositions possessed by fish relative to most benthic invertebrates. Combining fish and benthic invertebrates provided a more robust data set for exploring food web patterns at a scale that acknowledged the importance of fish–invertebrate interactions for food web functioning. However, potentially patchy fish distributions may have obscured some patterns that would have otherwise been evident if benthic invertebrates were considered alone. In this regard, the chosen trait modalities helped identify stations where high relative biomasses of hyperbenthic taxa may have biased community-weighted mean trait compositions.

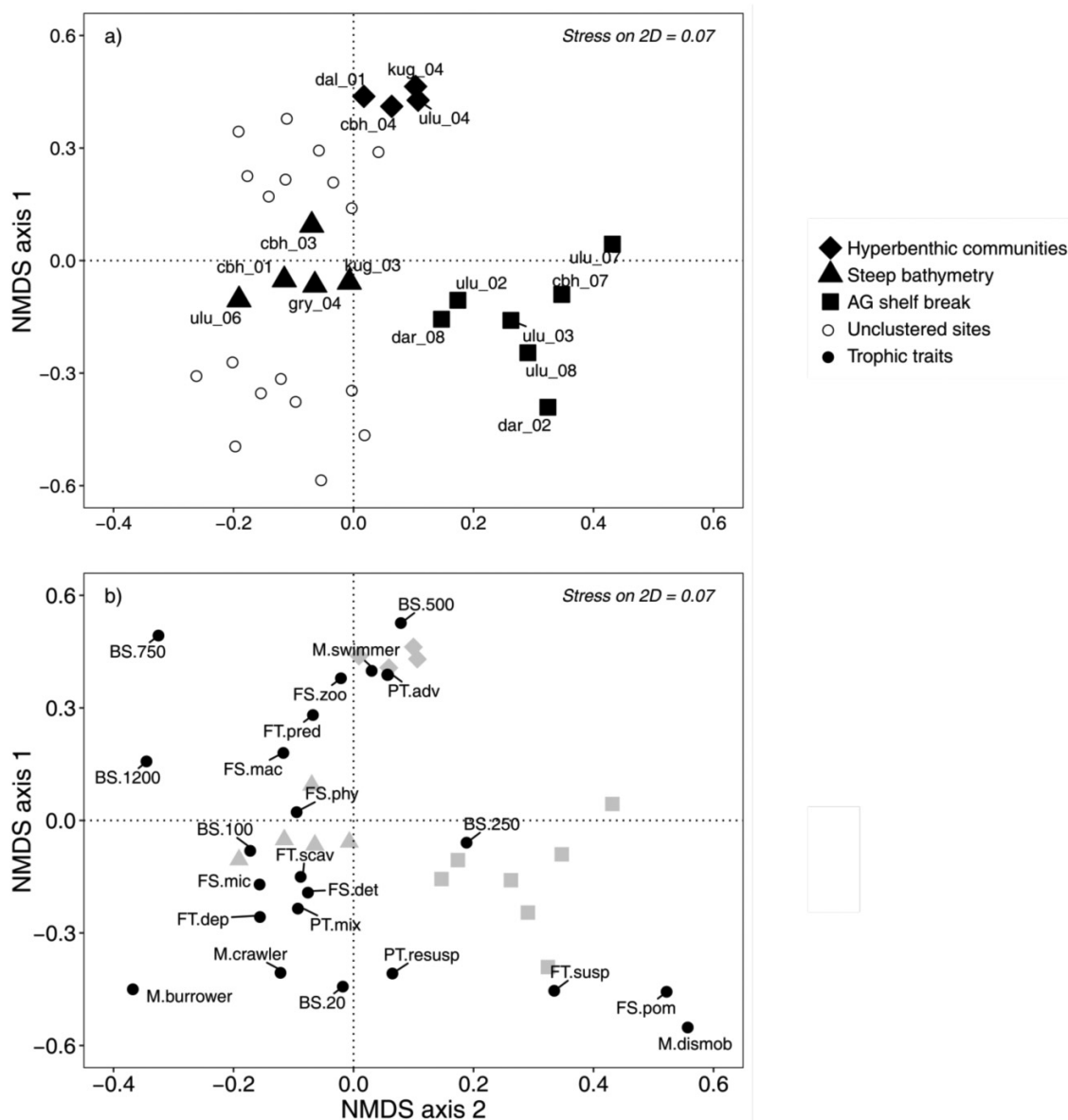
Contrary to our prediction, the distribution of trophic traits was not significantly related to sedimentary proxies for organic matter delivery to the benthos. The relationships between trait structure and bottom oceanography identified by the RLQ-fourth corner analysis may have simply reflected an increasing incidence of organisms with strong swimming ability at deeper depths, where there are lower oxygen concentrations and higher temperatures. Fish reached maximum total abundances around 500 m depth (Majewski et al. 2017; but not necessarily relative abundances compared to benthic invertebrates; see Supplementary Material 3). Alternatively, higher bottom oxygen concentrations may have promoted higher macrofaunal density and species diversity in shallower habitats, as has been previously observed in the

region (Roy et al. 2014), possibly linked to a positive influence of bottom oxygen concentrations on sediment nutrient cycling (Link et al. 2013b). Recent investigations of Arctic benthos suggested that some aspects of food web structure and function, such as benthic remineralization, taxonomic diversity, and benthic–pelagic coupling, are influenced by organic matter input regimes (Tamelander et al. 2006; Link et al. 2013b; Roy et al. 2014; Stasko et al. 2018a). We therefore expected the distribution of trophic trait modalities to directly respond to indices of benthic food supply (e.g., high abundance of traits promoting the rapid digestion of freshly deposited food where benthic Chl *a* indicated high phytodetrital inputs; Link et al. 2013b). If episodic processes that influence food availability are indeed linked to regional patterns in trophic trait diversity, as hypothesized above, then sedimentary proxies for benthic food supply would not be expected to reliably reflect those processes. Sedimentary evidence of pulsed organic matter inputs can be short-lived. For example, benthic invertebrates can consume newly sedimented organic matter from phytoplankton blooms within a few weeks, leaving little evidence in the sediment to be measured as part of a regional gradient (Renaud et al. 2007; Link et al. 2013b).

In large heterogeneous areas, attempts to link specific environmental variables to trait composition may be hampered by local habitat complexity (e.g., Moretti et al. 2009; Roy et al. 2014). The premise of linking traits to environmental gradients assumes a strong role in habitat filtering, wherein a set of abiotic and biotic constraints determine which trait modalities persist in a given location (Keddy 1992). It is possible that the relevant habitat filters acting at local scales on Arctic shelves are not captured by variables measured at regional scales. This is an important consideration when scaling monitoring programmes up from local to regional.

Regardless, stations exposed to similar abiotic forcings had similar trophic trait compositions, even though we lacked statistical descriptions of the specific, underlying trait–environment relationships. Moreover, the composite measures of trophic trait diversity (especially FDis and

Fig. 6. Non-metric multidimensional scaling (NMDS) ordination of (a) stations and (b) traits. Stations belonging to significant clusters identified by hierarchical cluster analysis of community-weighted mean trait values are shown as black symbols in (a) and as grey symbols in (b) to illustrate cluster associations with trait values. Codes for trophic functional traits are defined in Table 1. The distribution of stations relative to traits in NMDS ordination is aligned closely with the results of hierarchical clustering and IndVal analyses that assigned indicator traits to each cluster.



community-weighted trait compositions) revealed unique information compared to analogous taxonomic diversity and stable isotopic diversity metrics, aside from a strong linear relationship between taxonomic and traits-based species richness. Our findings add to growing evidence that monitoring approaches that consider emergent patterns in trait composition are more powerful tools for detecting community change than those based on isotopic or taxonomic diversity indices alone (Mouillot et al. 2013; Włodarska-Kowalczyk et al. 2019; Al-Hababeh et al. 2020; Martini et al. 2021). In marine systems, trait-based approaches are well-developed and widely used for benthic communities and could be useful for monitoring the effects of changing energy pathways to

upper trophic levels. This may be true even for consumers more closely linked to pelagic pathways because benthic communities are likely to respond to the same processes expected to enhance pelagic production and vertical flux along the Beaufort Sea slope, such as decreasing summer ice extent, increasing heat content, and reduced stratification (Bluhm et al. 2020; Polyakov et al. 2020; Yunda-Guarin et al. 2020). For example, the Eastern Beaufort Sea beluga whale population is key to conservation objectives for the Tarrim Niryu-tait and Anguniaqvia niqiqyuam MPAs. Continental slope areas at 200–500 m depths, where we observed regionally high trait-based trophic diversity, are important summer foraging habitat for beluga whales in the region, thought to be driven

by the occurrence of their preferred prey, adult Arctic Cod (*Boreogadus saida*) (Loseto et al. 2006; L. Storrie, personal communication, 2021).

Indices of food web structure based on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ have been used for more than two decades, but they do not provide a framework for considering species' relative biomasses (Bearhop et al. 2004; Layman et al. 2007). Rigolet et al. (2015) argued that omitting biomass distributions from isotopic trophic indices ignored the role of energy flow, and in doing so distorted the relative importance of trophic processes. Biomass-weighting isotopic indices reduce the influence of less abundant species so that trophic diversity is not erroneously inflated by rare species feeding at the margins of available organic matter sources. Many benthic species can exhibit substantial feeding plasticity, and thus likely derive their carbon from the most readily available sources (Renaud et al. 2007; North et al. 2014; Mäkelä et al. 2018). If this is the case, isotopic diversity (a relative measure) could exhibit low regional variability despite significant differences in the importance of isotopically distinct organic matter sources to benthic communities in the Canadian Beaufort Sea and Amundsen Gulf (Stasko et al. 2018b). Such a mechanism could explain the lack of correlation between isotopic diversity and both traits-based diversity and taxonomic diversity. For example, Włodarska-Kowalczyk et al. (2019) found no significant differences in a variety of isotopic niche metrics calculated for two Arctic fjord benthic communities despite large differences in species and trait richness, and differences in the placement of isotopic niches along the $\delta^{13}\text{C}$ continuum.

The joint use of traits-based and isotopic functional diversity did not reveal the strong differences in food web diversity expected between the Beaufort Sea and Amundsen Gulf, and we did not find strong linkages between trophic traits and proxies of benthic food supply. Instead, our findings suggested that (1) most benthic communities across the Canadian Beaufort Sea and Amundsen Gulf relied on a similar diversity of sedimentary organic matter sources as indicated by isotopic diversity, but (2) shelf-edge and upper-slope communities maintained relatively high trophic trait diversity to exploit pulsed food inputs. Analogous traits-based, isotopic, and taxonomic diversity metrics were not correlated with each other, with the exception of traits and taxonomic richness, suggesting that each approach provided unique and complementary information about food web structure. More studies are needed to establish whether high trophic trait diversity is characteristic of interior Arctic shelf-break communities, whether this finding is consistent if fish and benthic invertebrates are considered separately, and whether indices of dynamic food delivery not explored here can be linked to trait diversity or composition. Such further study will aid predictions of climate-induced changes to benthic food web structure.

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Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/AS-2021-0040>.

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