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ABSTRACT

Climate change is challenging species' abilities to respond and function. In the Arctic, shifts in temperature and ice cover are disrupting established biological interactions and thereby ecosystem structure and function. By examining epibenthic communities in coastal and continental shelf habitats of Northeast Greenland that have been ice-locked for centuries, we provide a contemporary baseline of benthic functional diversity through a trait-based approach. We show clear trends in biodiversity and traits from *a priori* defined groups of fjord, shelf, shelf break, and slope habitats. With biodiversity and functional indices, we identified how fjord and shelf communities could be vulnerable to current and future changes in climate conditions. Using a hierarchical model of species communities (HMSC) we found taxa occurrences, regardless of taxonomic relatedness, were mainly driven by changes in depth, salinity, and oxygen and less so by temperature. Though rising global temperatures are undoubtedly altering the physiochemical structure of the shelf area, our study underscores the significance of often-overlooked environmental factors in Arctic climate change studies. Moreover, we highlight how species traits have a significant role in forming and maintaining community composition by explaining a high amount of among-taxa variation in taxa occurrences and taxa responses to the environment. While the significance of this is not known in relation to community resilience, as Arctic shelf processes intensify (*e.g.,* Atlantification), changes in benthic communities and their ecological roles will ultimately affect ecosystem functioning and the broader dynamics of complex seascapes.

1. Introduction

Spatially complex seascapes, such as continental shelves in the high Arctic, have a significant role in the broader dynamics of marine ecosystems due to the ecological interactions between diverse biological communities and their environment. Benthic invertebrates inhabiting the seafloor play a major functional role in the Arctic marine ecosystem, where they contribute to services such as nutrient recycling and carbon sequestration, as well as the stability of the ecosystem (Grebmeier et al., 2015; Solan et al., 2020). Yet, due to climate warming, happening at rates four times faster in the Arctic compared to anywhere else on Earth

(Pachauri and Meyer, 2014; Mouginot et al., 2019; Rantanen et al., 2022), benthic communities and their ecological roles are subject to rapidly shifting physical and biogeochemical conditions. Changes in sea ice cover, water temperature, and primary productivity are affecting benthic species, both physiologically and competitively (Renaud et al., 2015; Slagstad et al., 2015; Degen et al., 2018). Such environmental change is likely to impact Arctic benthic marine community structure and function, with possible implications for ecosystem services such as carbon storage and fisheries (März et al., 2021).

While there have been multiple studies addressing the benthic faunal composition of Northeast Greenland in fjords, shelves, and slopes (to

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name a few: Mayer and Piepenburg, 1996; Piepenburg, 1988; Sejr et al., 2000, Włodarska-Kowalczuk et al., 2012; Fredriksen et al., 2020, Vedenin et al., 2022), no study has yet addressed the functional composition of Northeast Greenland benthos in detail. This area is important to study since it is typical of an Arctic shelf with ice still present all year round (albeit diminishing at rapid rates during summer periods) as well as belonging to the world's largest national park, implying a pristine environment to investigate naturally occurring species assemblages. Furthermore, it is exposed to increased stratification through runoff from the Greenland ice sheet (Sejr et al., 2017; Mouginot et al., 2019) and warming from the Return Atlantic Current occurring across the continental shelf resulting in Atlantification (Gjelstrup et al., 2022). Where time series are absent, such as for the benthos in Northeast Greenland, spatial gradients of functional diversity can be informative for monitoring the stability and shifts in seafloor composition and function (Renaud et al., 2015; Al-Habahbeh et al., 2020; Solan et al., 2020).

A modern approach to gaining insights into ecological functioning from a species' community and the environment is through Biological Trait Analysis (BTA). A species trait describes an organism's effect on or response to the environment via its morphology (*e.g.,* body form), behaviour (*e.g.,* feeding habit), physiology (*e.g.,* temperature tolerance), and life history (*e.g.,* larval development) and the approach is widely applied in benthic ecology to understand the mechanisms of community assembly and functioning (Bremner et al., 2003, 2006; Degen and Faulwetter, 2019). While the assembly of species communities occurs through niche partitioning, where species coexist by occupying different ecological preferences (MacArthur and Levins, 1967), species traits determine the species' capacity to access and exploit different resources, resist physical disturbance, and tolerate stress, which ultimately influences community assembly via composition and structure. Thus, species occurrences and their traits are a product of speciation (genetic evolution), dispersal (migration and advection), and community dynamics, which are correlated with the fitness of the species and their coupling with geographic constraints and physical characteristics of the environment (*e.g.,* preferences for habitat type, water temperature, salinity, and depth) (Díaz et al., 2013; Ovaskainen and Abrego, 2020). Modern statistical approaches recognise the importance of traits in community assembly and are now able to test for the underlying mechanisms that structure biological communities by quantifying to which extent traits contribute to species responses to environmental variables (Tikhonov et al., 2020). This approach offers a greater mechanistic understanding of the stochastic and deterministic processes that drive species occurrences, co-occurrences, and their traits and can aid in predicting how benthic functioning responds to prominent ecological changes, such as those found to occur in Arctic coastal and continental shelf ecosystems.

Here, we investigate the trait diversity and composition of epibenthic communities of the Northeast Greenland continental shelf, from fjord to slope habitats, and assess the environmental attributes that may influence taxa and their traits using the novel ecological community analysis, Hierarchical Modelling of Species Communities (HMSC) (Tikhonov et al., 2019). HMSC integrates multiple data types and captures the underlying processes of community assembly via a trait-based filtering approach. This results in showing distributions of traits and trait selection across space given the environmental covariates and species composition. The framework also includes taxa relatedness (in a taxonomic tree) to account for evolutionary constraints in species' responses to the environment by finding taxonomic correlations of species responses to the environment after accounting for the species traits. Therefore, HMSC analysis is a powerful tool for understanding the dynamics and responses of biological communities with traits.

In addition to being the first inventory of functional benthic diversity across these habitats, the aims of this study are to 1) identify whether established taxonomic assemblages across the fjord, shelf, shelf break, and slope of Northeast Greenland show spatial distinctions in functional

composition and diversity, 2) use indices that assess species composition and their traits to highlight any potentially vulnerable (or resilient) communities, and 3) gain a better understanding of the drivers across the continental shelf in relation to spatial trait composition and reveal what this means in light of climate change. We postulate that there will be spatial distinctions in the trait-based structure related to habitat characteristics; see Table 1 in the methods section for specific expectations of trait distributions across the habitats.

2. Materials and methods

2.1. Study site and sampling

Epibenthic megafaunal invertebrate data were collected as part of the TUNU Programme (Christiansen, 2012) at The Arctic University of Norway, UiT, in 2015 (TUNU-VI) and 2017 (TUNU-VII). Collection is described in detail by Fredriksen et al. (2020). Briefly, onboard the R/V Helmer Hanssen, the semi-quantitative Campelen 1800 shrimp trawl was used to estimate the number of epibenthic species and their abundance in 2015 and 2017 and their biomass in 2017. Abundance and biomass estimates were standardised to the number of individuals (ind.) and gram wet weight (g ww) per 1000 m^{-2}, respectively. A total of 18 stations, with a sampling depth range of 65 m–1011 m, were sampled across the Northeast Greenland shelf including Bessel Fjord, Dove Bugt, and Belgica Bank, with other stations located along the shelf, shelf break, and upper continental slope (Fig. 1, Supplementary Material (SM) App.1 Table S1). The original dataset consisted of 274 epibenthic invertebrate taxa. As identification at the species level was not always possible, we deduced the data to the closest taxonomic level, leaving 120 individual taxa, 120 taxa with recorded abundances (2015 and 2017) and 104 also with biomasses (2017). Phyla diversity is represented in SM (App 1. Fig. S2). Taxa were checked and updated with the current nomenclature in the World Register of Marine Species (WoRMS; https://www.marinespecies.org/. Accessed: April 2023).

2.2. Environmental variables

The following environmental variables were recorded at each station: water depth (m), near-bottom temperature (°C), bottom salinity, bottom oxygen concentration (ml L^{-1}), fluorescence and turbidity (FTU) (Fig. 1 C) (SM App. 1 Table S3). These variables were recorded by a Sea-Bird Electronics SBE-911 conductivity-temperature-depth (CTD) profiler. Additionally, stations were categorised into geographical habitats defined by Fredriksen et al. (2020) as fjord, shelf, shelf-break, and slope. Here, we used these habitats to analyse spatial distributions of trait composition, species, and functional indices.

2.3. Trait-based approach

To examine spatial differences in trait composition, nine traits were selected, with three traits each representing behavioural, life history, and morphological characteristics, to capture different trait expressions across taxa (*e.g.,* 4 categories of feeding habit) (Table 1). For consistency across Arctic trait-based studies, trait information was collected from the Arctic Trait Database (https://www.univie.ac.at/arctic traits/, Accessed: April 2023). If traits were not available from the Arctic Trait Database at the lowest taxonomic rank, the literature was reviewed to retain the highest taxonomic resolution possible, or the trait was given a score of zero in order not to bias results. For the final trait list of the 120 individual taxa; 64 were identified down to species level, 32 to genus level, 8 to family, 5 to order, 8 to class, and 3 to phylum level (for taxa-trait matrix, see SM, Fig. S4). We used the fuzzy coding approach to account for taxa's ability to perform various categories within a trait. Thus, taxa were assigned one or multiple categories based on their affinity to these, according to a 0−3 scoring system, where 0 means no affinity and 3 is a high affinity to a category (Chevene et al., 1994). Taxa

Table 1

Arctic epibenthic traits: expected spatial distribution and ecological significance.

Trait	Categories	Ecological Function	Expected spatial distribution
Body size (maximum; adult) **(Morphology)**	S1 Small <10 mm S2 Small–medium 10–49 mm S3 Medium 50–99 mm S4 Medium–large 100–299 mm S5 Large >300 mm	Directly links to metabolic rates but indirectly with many ecosystem functions including productivity, food webs, carbon sequestration, sediment oxygenation, and habitat structuring.	Size is impacted by depth, temperature, and food availability. As an increase in size is usually correlated in colder waters, such as the fjord and shelf, these habitats may have larger organisms compared to the slope. References: 1–7
Body form **(Morphology)**	BF1 Globulose	Associated with ecological roles in sediment transport, habitat structuring, or bioengineering sediment and/or nutrients. Often a proxy for taxonomy or habitat quality.	Body forms are often coupled with the environment: sediment type, currents, etc., and so distinctions across the habitats may be seen but difficult to predict. Due to the high number of Porifera in the dataset, various forms may be found.
	BF2 Vermiform BF3 Dorsoventrally compressed BF4 Laterally compressed BF5 Upright	References: 8–9	
Skeleton **(Morphology)**	SK1 Calcareous SK2 Siliceous SK3 Chitinous SK4 Cuticle SK5 None	Indicative of environmental quality and at-risk communities (ocean acidification/ trawling/prey etc.). Related to Inorganic carbon sequestration (*i.e.,* calcifying taxa contribute most)	An earlier analysis represents areas of bivalve dominance (shelf banks), ophiuroid and asteroid dominance (Fjord), and Arthropoda (shelf) which should be mirrored in the trait analysis (e.g. chitinous versus calcareous) (Fredriksen and others, 2020). References: 8, 10
Larvae development **(Life history)**	LD1 Pelagic/ planktotrophic LD2 Pelagic/ lecithotrophic LD3 Benthic/ direct	Nutrient recycling/ productivity between pelagic and benthic zones, dispersion, and recovery capabilities.	Planktotrophic larvae are rarely found in polar fjords and shelves but are likely to increase with warmer water such as the shelf break and Slope. Direct development is correlated with food availability and therefore more likely on the fjord or shelf. References: 9,11–14.
Reproductive method **(Life history)**	R1 Asexual R2 Sexual: external	Food availability to the benthic/pelagic realm, resource	Asexual reproduction can occur because of

Table 1 (*continued*)

Trait	Categories	Ecological Function	Expected spatial distribution
	R3 Sexual: Internal brooding	facilitation, carbon transportation, and dispersion and recovery capabilities.	sudden changes in the environment such as salinity and temperature, and thus, more possible in the fjord. Internal sexual reproduction could be less common across habitats on the East Greenland continental shelf, where the dynamic seafloor environment (with strong currents, sills, and troughs) may make it difficult for individuals to locate mates. Therefore, brooding and external fertilization may be more favourable in such habitats. References: 13, 15-16
Mobility **(Life history)**	MO1 None MO2 Low MO3 Medium MO4 High	Ability to avoid predators, find resources, and dispersal capabilities. Limited mobility can contribute to habitat complexity.	At the slope and in some areas of the shelf, food may be scarce or patchy, and therefore, an increase in more mobile individuals may be seen compared to the fjord. References: 8, 16
Adult movement **(Behaviour)**	MV1 Sessile/ none MV2 Burrower MV3 Crawler MV4 Swimmer	Metabolic requirements, trophic pathways and dispersal/ recolonisation potential.	Similar to Mobility; large areas where food may be limited or patchy may mean a greater number of crawlers or swimmers. High organic content and/or nutrients in the fjord and shelf may support sessile organisms. References: 8,16-19
Feeding habit **(Behaviour)**	FH1 Deposit FH2 Filter/ suspension FH3 Opportunist/ scavenger FH4 Predator	Production, nutrient cycling, trophic structure/ energy fixation or transfer. A good indicator of hydrological conditions.	If feeding habits correlate with mobility and movement, fast-moving swimmers and crawlers, then predators will be a more likely to increase on the slope. References: 8–9, 11, 16-18
Zoo-geography **(Behaviour)**	Z1 Arctic Z2 Arctic-boreal Z3 Boreal Z4 Cosmopolitan	Species distribution ranges; species vulnerability and potential range expansion.	Currents and warmer water along the slope and shelf break may mean more boreal or cosmopolitan species compared to the fjord and

Table 1 (*continued*)

Trait	Categories	Ecological Function	Expected spatial distribution
			shelf. References: 8

with equal affinity to several categories within a biological trait were assigned the same score for those categories. Both the taxa - trait matrix and taxa - abundance and biomass matrices were then used to determine the spatial distributions of traits and characterise the functional diversity across the high Arctic shelf ecosystem.

2.4. Spatial comparison of taxonomic composition to community trait combinations

For community comparisons, the trait-abundance and trait-biomass matrices were (separately) used to calculate trait community weighted means (CWM) for each station using the 'FD' package in R (Laliberté et al., 2014). Overall spatial trait trends are represented as cumulative percentages of the CWM. Furthermore, multivariate analyses (Non-metric Multidimensional Scaling; nMDS) of community taxa data and trait CWM values were performed using the 'vegan' package

(Oksanen et al., 2020). To reduce the impact of highly abundant species in the data, a square-root transformation was applied to both the abundance and biomass data before computing a Bray-Curtis similarity matrix. A Gower similarity matrix was applied to the trait CWM datasets. A Permutational Multivariate Analysis of Variance (PERMANOVA) was performed to determine any significant differences in taxa and traits composition across the different habitats. As the analysis builds on variation within and among groups, the single station representing the shelf break in the biomass data was excluded. All analyses were conducted using the statistical computing software R v.3.5.1(R Core Team, 2021).

2.5. Indices assessing diversity, vulnerability and resilience

For biodiversity indices, taxa richness and diversity were calculated using the 'vegan' package in R (Oksanen et al., 2020). Species diversity was calculated as the Gini – Simpson Index $(1 - \lambda)$ where λ is the probability of finding the same species within a sample, weighted by abundance, with values ranging from 0 (no diversity) to 1 (maximum diversity). Functional trait metrics were calculated using the 'FD' package (Laliberté et al., 2014), measuring functional richness as a convex hull volume describing trait space occupied by taxa. Functional
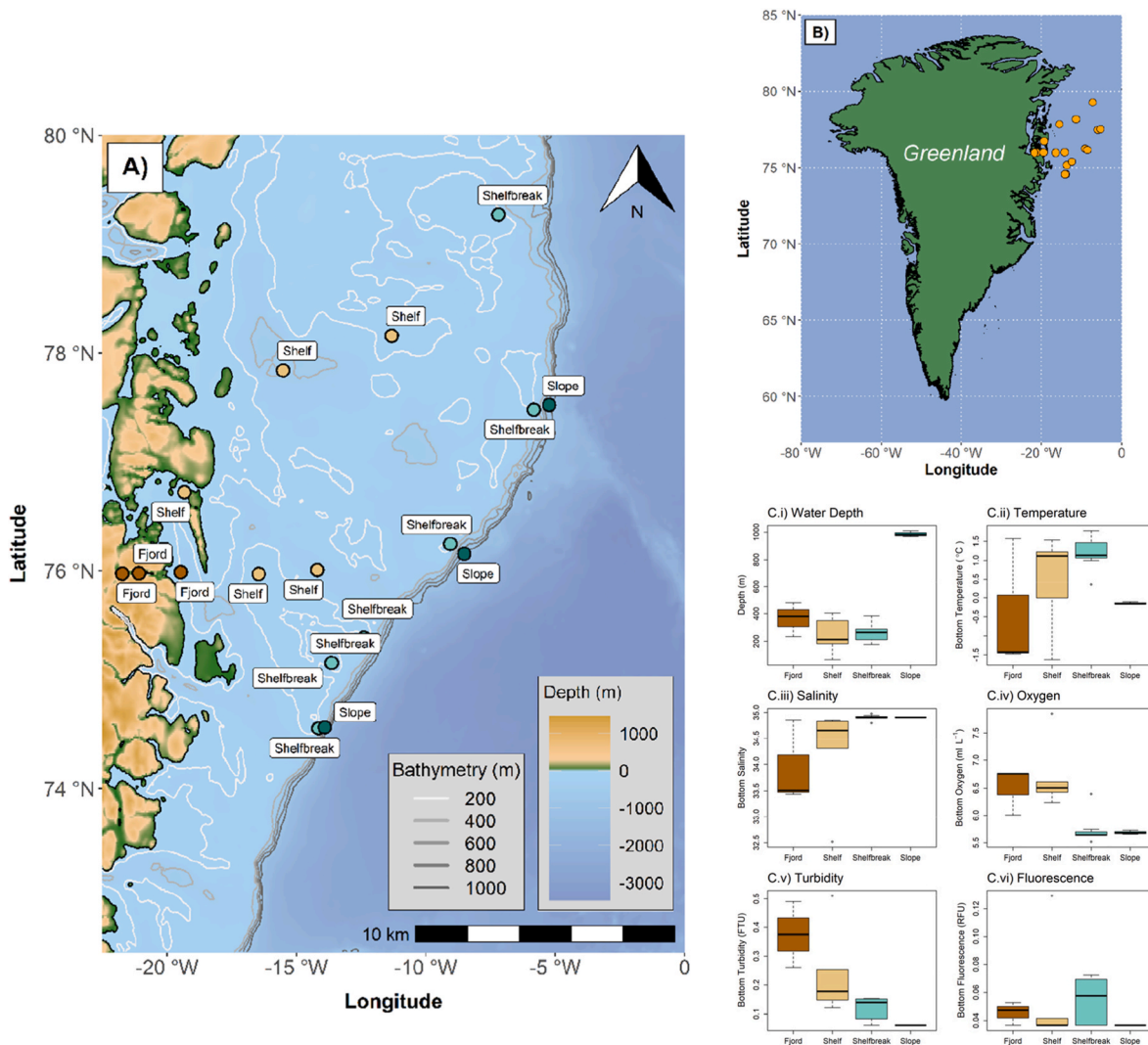

Fig. 1. Study area. A) Map of the 18 stations sampled across the Northeast Greenland Shelf. Contour lines represent bathymetry up to 1000m, and B) overview of Greenland and the location of the respective stations, and C) environmental variables used in the analyses including i) water depth (m), ii) bottom water temperature, iii) bottom salinity, iv) bottom oxygen (ml L^{-1}), v) turbidity (FTU), and vi) Fluorescence (RFU).

divergence, selected based on its likeliness in description and scale (0–1) to taxa diversity (from now on referred to as functional diversity), relates to how abundance is distributed within the volume of functional trait space occupied by species (Laliberté and Legendre, 2010). Additional diversity metrics, taxa vulnerability and functional redundancy, were computed following Ricotta et al. (2016) using the 'adiv' package (Pavoine, 2021). Taxa vulnerability estimates extinction probability based on taxa rarity and functional similarity (*e.g.,* a taxon would be more vulnerable if it is rare in occurrence and in its function), while functional redundancy identifies communities with a surplus of a given function based on taxa abundance or biomass. All indices, collectively offering insights into community dynamics, were statistically tested across habitats using ANOVA and Tukey's post-hoc test. Prior to statistical testing, homogeneity of variance was assessed with the Levene test, and transformations were applied when necessary, including log and square transformations for taxa richness and vulnerability, respectively.

2.6. Drivers of ecological communities; traits, environment, and taxonomy

HMSC belongs to the class of joint species distribution models (Warton et al., 2015). One advantage of this framework is that it integrates a hierarchical layer for how taxa responses to environmental covariates depend on species traits and phylogenetic relationships (Abrego et al., 2017). HMSC uses multivariate hierarchical generalised linear mixed models fitted with Bayesian inference. Our model inputs include taxa occurrence data as response matrix, the six environmental covariates (water depth, bottom temperature, bottom salinity, oxygen, turbidity, and fluorescence) as explanatory covariates, as well as species traits, and a taxonomic tree to account for phylogenetically structured constraints in species responses. Collinearity was tested between environmental variables, and while some correlations (where $R^2 \geq 0.7$ or ≤ -0.7) were found between salinity and oxygen, fluorescence, and turbidity (SM Fig. S5), the decision to retain all variables in our analysis was made after performing model selection including and excluding the collinear variables. Using WAIC (Widely Applicable Information Criterion, similar to AIC but suitable for JSDMs) as the model selection criterion, the full model, which included all covariates, showed the lowest WAIC values and was therefore the most parsimonious model (SM Table S6). Furthermore, we examined model-specific variance partitioning to investigate whether, for example, the removal of fluorescence would result in a disproportionate increase in the explained variation of salinity. Should this be the case, it could be assumed that both covariates competed for the same signal in the model, sharing some explained variation. However, as this was not the case, it indicates that each covariate carried unique information and that collinearity did not unduly bias the model outcomes. Each station was used as a sampling unit and spatial (*e.g.*, latitude and longitude) or temporal structures were excluded due to model complexity and the sample size. As taxa incidence was low across stations, the data was zero-inflated. Thus, we opted for a model where all data were converted into presence-absence, applying a probit regression model with fixed environmental effects and random station and habitat effects. The taxonomic tree was constructed using the 'taxize' package in R (Chamberlain et al., 2020) and based on the open-access database from Global Biodiversity Information Facility (GBIF) for taxa information (https://www.gbif.org/, Accessed: March 2024). Taxonomic correlation (ρ) in HMSC ranges from 0 to 1, indicating independence (0) to full taxonomic influence (1) on ecological niches.

The model is fitted with Bayesian inference, and hence employs posterior sampling, via Markov chain Monte Carlo (MCMC) simulations. The default priors were applied (Ovaskainen and Abrego, 2020; Tikhonov et al., 2020), and the posterior distribution was sampled with 4 Markov chain Monte Carlo (MCMC) chains, each run with 375,000 iterations, where 125,000 were deleted as burn-in, and were additionally thinned by 1000. Per chain, 250 posterior samples were taken, resulting in a total of 1000 posterior samples. MCMC convergence was checked

via the potential scale reduction factors (Gelman diagnostic (Gelman and Rubin, 1992) for both the beta (relationship between taxa and the environment) and gamma (relationship between traits and the environment) parameters (Ovaskainen and Abrego, 2020). The models' fit was assessed using coefficients of discrimination (Area Under the Curve, AUC, and Tjur's R^2) which indicate how well the occurrence probabilities discriminate taxa at each sampling unit as either present or absent (Pearce and Ferrier, 2000; Tjur, 2009). An AUC at 0.5 (or a Tjur R^2 of 0), means the model is no better than chance, but an AUC (or Tjur R^2) closer to 1 means the model is performing well and can accurately discriminate between present (1) and absent (0) taxa at the sampling level. The beta, gamma, and rho parameters were then examined for relationships between taxa, traits, the environment, and taxonomy and the explained variation for each taxon was then partitioned between fixed and random effects (Ovaskainen and Abrego, 2020). To evaluate the predictive power of the model we performed a four-fold cross validation procedure, where each fold was randomly assigned among sites. All analyses were performed in the Hmsc package in R, v3.0-9 (Tikhonov et al., 2020).

3. Results

3.1. Spatial comparisons of taxonomic composition to community trait combinations

We found divergent trait composition across the different Northeast Greenland habitats, following dissimilarities in taxonomic composition (Fig. 2). The taxonomic structure differed significantly between habitats (PERMANOVA; abundance: $DF_{3,14}$, $F = 2.13$, $R^2 = 0.31$, $P = 0.001$ | biomass: $DF_{1,7}$, $F = 2.15$, $R^2 = 0.26$, $P = 0.024$) as did traits for the abundance data (abundance: $DF_{3,14}$, $F = 2.13$, $R^2 = 0.36$, $P = 0.008$ | biomass: $DF_{1,7}$, $F = 1.99$, $R^2 = 0.25$, $P = 0.11$). *Post-hoc* pairwise tests revealed significant differences in taxonomic composition between the shelf-break and slope habitats (abundance: $F = 2.25$, $R^2 = 0.18$, $P = 0.04$) and between the fjord and shelf habitats (biomass: $F = 2.15$, $R^2 = 0.26$, $P = 0.02$), but none for the traits ($P > 0.5$). For full pairwise statistics see SM App. 1 Tables S7.1 and S7.2.

Gradual changes in the CWMs between neighbouring habitats (fjord, shelf, shelf break, slope) were more clearly seen in the abundance dataset than that of the biomass (Fig. 3). For example, trait expression for body size in the abundance data shifts from a higher proportion of small–medium and medium body sizes in the fjord and shelf, to a medium and medium–large body size on the shelf break and slope. Similar shifts across habitats in categories can be found for adult movement, feeding habits, larval development, reproduction, skeleton type, and zoogeography (Fig. 3). The trait CWMs for the biomass dataset did not show such clear shifts in trait composition. In comparison, the modalities were equally distributed across the habitats (see body size and reproduction, for example (Fig. 3)). Additionally, the abundance and biomass datasets revealed contrasting proportions in trait composition, such as biomass having almost no globulose body form present on the shelf break as well as having a higher proportion of siliceous skeleton on the fjord and shelf. Additionally, a larger proportion of sessile taxa were shown in the biomass analysis than in the abundance one.

3.2. Indices assessing diversity, vulnerability, and resilience across habitats

Taxa richness, vulnerability, functional richness, diversity, and redundancy were all significantly different across habitat types, whereas taxa diversity did not differ significantly ($P = 0.14$) (Fig. 4, full ANOVA results in SM App. 1 Table S8.1 and test statistics for Tukey's *post-hoc* see Fig. S8.2; but note unequal sample size among habitats). Taxa richness was highest across the shelf communities (*e.g.,* maximum of 57 taxa found at station 1354), and lowest at the slope (station range between 6 and 11 individual taxa). The observed pattern in taxa richness was also repeated in functional richness but with more variation within the fjord
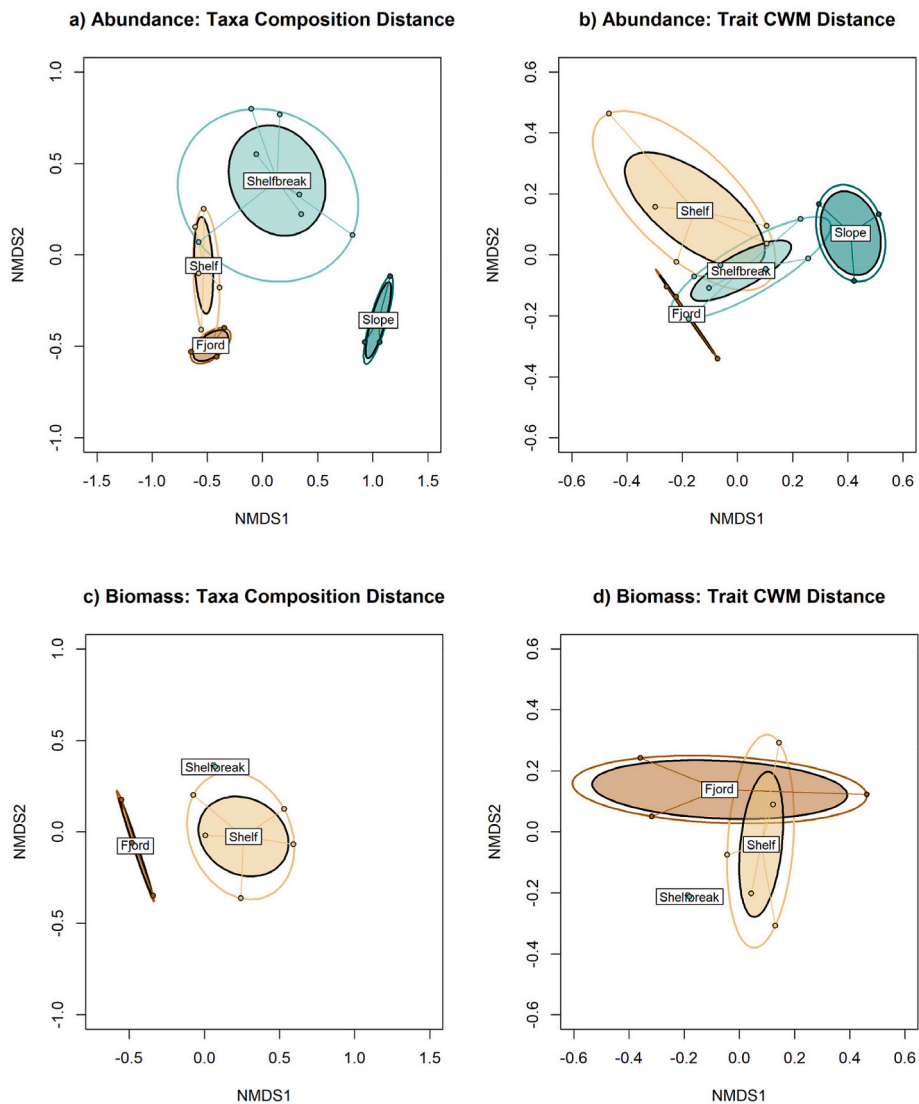
a) Abundance: Taxa Composition Distance

b) Abundance: Trait CWM Distance

c) Biomass: Taxa Composition Distance

d) Biomass: Trait CWM Distance

Fig. 2. Dissimilarities are shown between habitat groups (fjord, shelf, shelf-break, and slope) of epibenthic communities and their trait group assemblages. a) and b) show the dissimilarities in taxa and trait communities from the abundance data (number of individuals 1000 m^{-2}), while c) and d) show the dissimilarities from the biomass data (grams of wet weight 1000 m^{-2}). Small circles show station data points, while large, coloured circles represent the centrally weighted mean of the habitat groups, with the outer single-lined circle displaying the maximum values (variance). Note: Biomass was not recorded at slope stations (see methods).

and shelf groups (Fig. 4b). Taxa diversity was high across the fjord (mean Simpson Index ± SD = 0.76 ± 0.09, shelf (0.68 ± 0.27), and shelf-break (0.78 ± 0.15), with the lowest diversity occurring in the slope region (0.47 ± 0.22). This trend was similarly found for taxa vulnerability, although variability within habitats was much smaller than any of the other indices. Meanwhile, functional diversity was highest in the fjord and decreased with distance from the coast, being statistically significant from the shelf break and slope (Fig. 4e, *P* = 0.009). The reverse trend was observed in functional redundancy with the same significant relationship between the fjord and the slope (Fig. 4h, *P* = 0.01). Additionally, there was a positive relationship between functional richness and taxa richness (Fig. 4c, Estimate ± SE = 0.92 ± 0.11, T = 8.7, *P* < 0.0001, deviance explained = 82%), but no significant trend between functional diversity or functional redundancy and the number of taxa present.

3.3. Drivers of ecological communities

The HMSC model showed a good fit with average taxa *TjurR^2* (AUC) at 0.56 (0.98) (SD = 0.20 (0.04)) (Fig. 5) after all MCMC convergence

was satisfactorily met (SM Table S9.1 and Fig. S9.2). Generally, the ability to discriminate occurrences increased as taxa prevalence increased (SM Fig. S10.1). While the explanatory power of the model was good, the four-fold cross validation to evaluate the predictive power of the model resulted in low unsatisfactory values where many species occurrences were not better predicted than by random with an average predictive *TjurR^2* of 0.13 (SD = 0.25) and a predictive AUC of 0.65 (SD = 0.25) (SM Fig. S10.2).

The explained variation of taxa occurrences was further partitioned into fixed (environmental covariates) and random effects (habitat and station) used in the model (Fig. 5, SM Fig. S11). Bottom depth and salinity were highest in explaining the variation of taxa occurrences with a combined average across taxa of 46.5% (depth mean = 25.6% and salinity mean = 20.9%), but with high variability among taxa (SD = 19% and 12.5%, respectively) (Fig. 5, SM Fig. S11). Taxa that had a higher amount of explained variation by depth include predatory brittle and sea stars (*Lophaster furcifer, Ophiura sarsii, Poraniomorpha tumida* and *Ophiocten sericeum*) and were predominantly found on the shelf and shelf break. Oxygen was third in explaining taxa occurrence (mean ± SD = 17.9% ± 14.1%) and explained the most variation in the
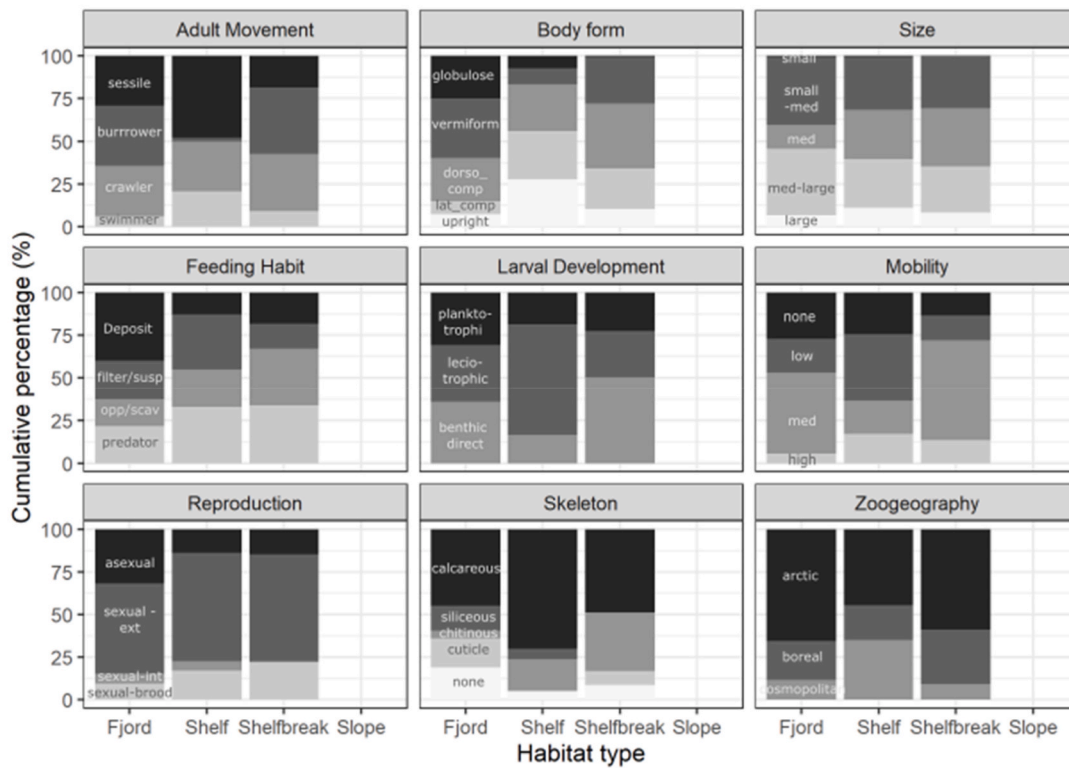
a) Abundance
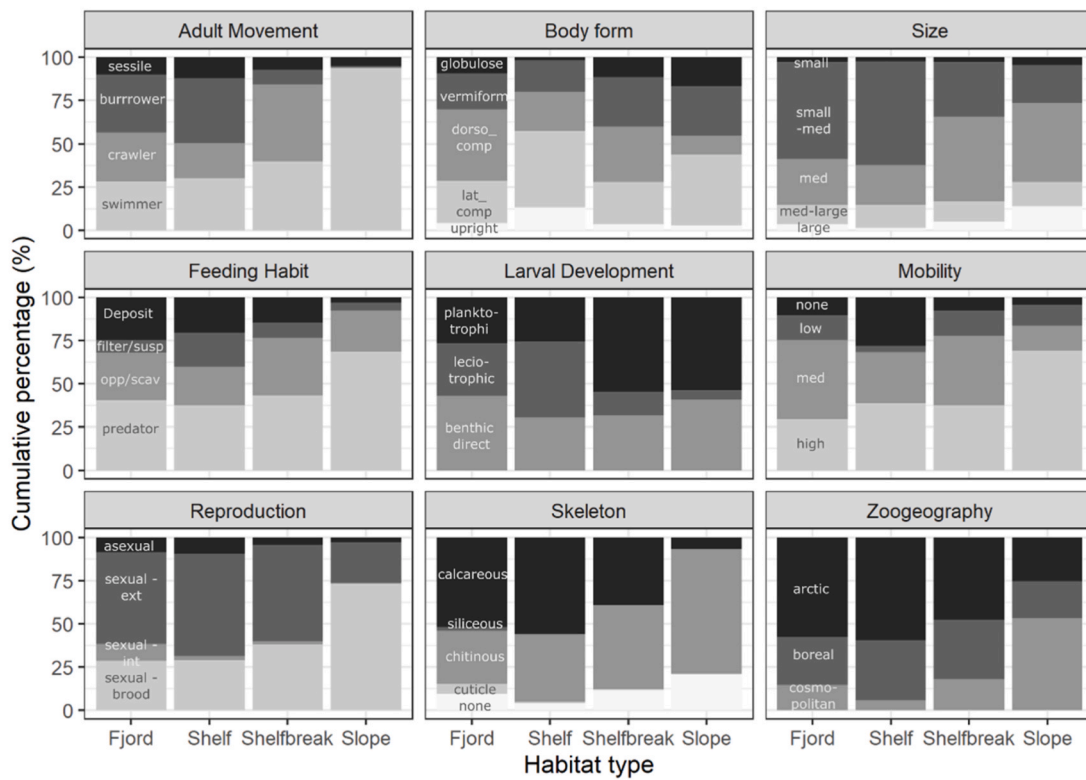
b) Biomass

Fig. 3. Community-weighted mean (CWM) values of exhibited traits for a) abundance and b) biomass data were converted into the cumulative percentages for each habitat type (fjord, shelf, shelf-break, and slope). See Table 1 for trait definitions.
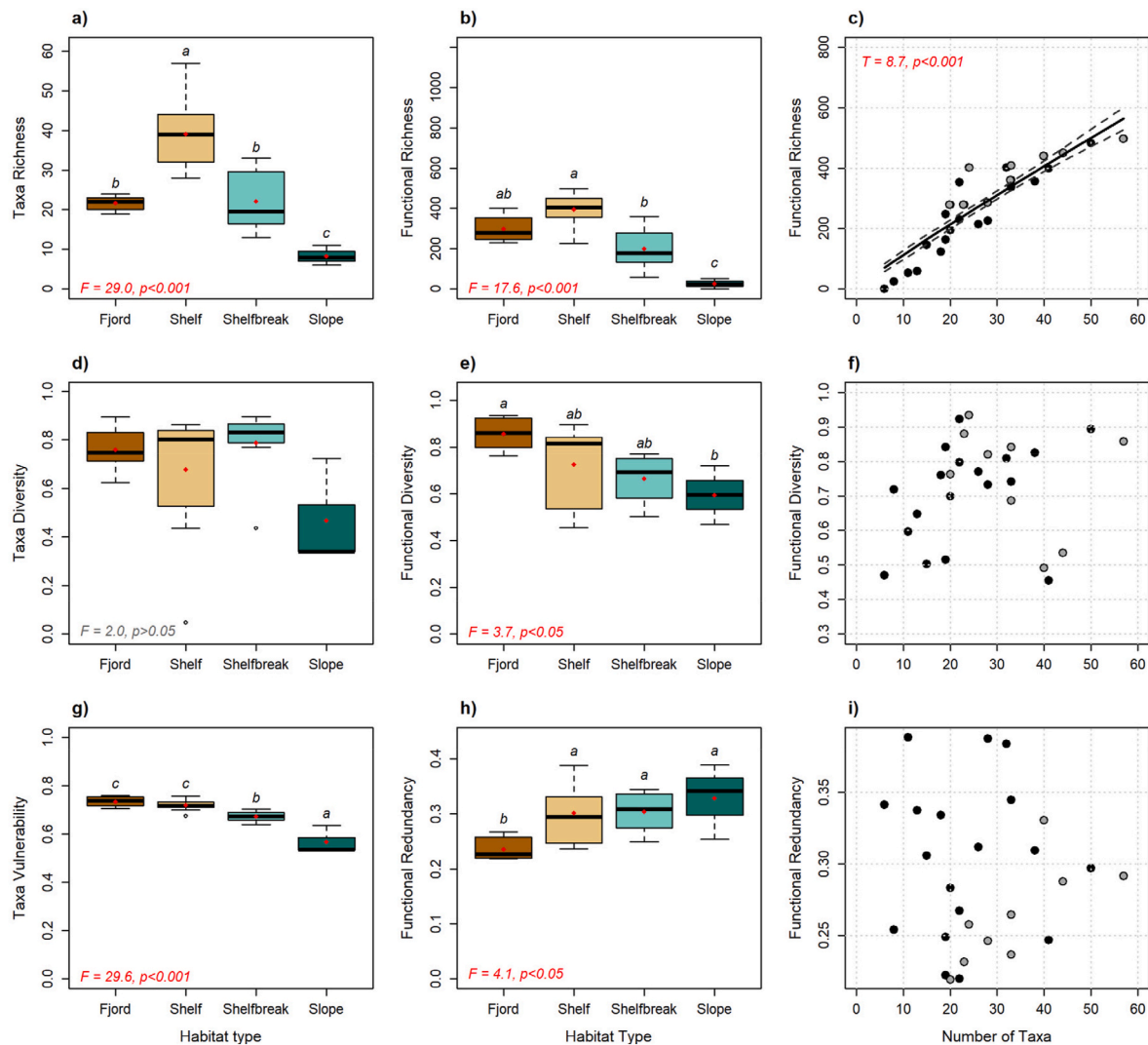
Fig. 4. Biodiversity and functional indices of the Northeast Greenland coast. Plots a), b), d), e), g), and h) show taxa or functional index and the relationship over habitats. Plots c), f), and i) display a functional index against the number of taxa. Functional Diversity is equal to Functional Divergence in the FD package. For box plots, the thick black line represents the median, boxes show 95% confidence intervals, error bars show the extent of the data outliers, and red diamonds signify the mean value. Letters represent Tukey's post-hoc significant differences between habitats. Those with the same letters are not significantly different to each other (for test variance see SM; Figure S7.2). For scatter plots, black-filled circles are abundance data points while grey-filled circles are biomass data points. A GLM significant trend is shown in c) with the upper and lower 95% confidence intervals represented with dashed lines. Significant test metrics are written in red (ANOVA for a, b, d, e, g, h, and GLM for c). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

occurrence of pycnogonids, *Boreonymphon* sp. (60%) and *Colossendeis proboscidea* (52%), and bryozoan, *Alcyonidium gelatinosum* (54%). Bottom temperature (12.1% ± 8.5%), turbidity (11.4% ± 9.0%), and fluorescence (10.5% ± 9.1%) explained a similar amount of variation in taxa occurrences. However, fluorescence had a particularly high amount of explained variance for filter-feeding Porifera (60% of explained variation). Meanwhile, the random effects, station and habitat, only accounted for very little variation in taxa occurrences (station = 1.1% ± 3.0% and habitat = 0.4% ± 0.4%). Therefore, of the proportion of the explained variation, the fixed effects of the model explained a mean of 98.4% of the variation in taxa occurrences, while the random effects combined explained a mean of 1.5%, suggesting that the environmental variables used as fixed effects capture most of the variation in taxonomic structure with little more to be explained by the habitat or station.

There was no evidence for related taxa to respond similarly to the environment. The posterior probability for similarity in the responses based on taxonomy was low $(Pr(\rho > 0) = 0.58; E(\rho = 0.18))$ (Fig. 6). Traits that are shared between taxonomic groups are shown in SM App. 1 Fig. S4. Regarding taxa responses to the environment, 44% of taxa

occurrences were negatively impacted with increasing depth, while increasing temperature and salinity positively increased 23% of taxa occurrences. Increased oxygen also had a positive response on 47.5% of taxa occurrences and increasing fluorescence negatively impacted 29% of taxa occurrences (Fig. 6). Interestingly, there was a mixed response to turbidity with 17.5% of taxa responding positively and 29% responding negatively (Fig. 6).

The gamma parameter, which measures the amount of among-taxa variation with regards to the taxa responses to the environment (*i.e.,* the fixed effects) and their traits, indicated that a relatively high amount of variation in taxa responses to the environment can be attributed to traits (γ-R^2 = 0.53). Furthermore, the proportion of explained variation between traits and the variation of taxa responses to the environmental variables were especially high for responses to oxygen, salinity, and turbidity (Table 2). Linear relationships between taxa traits and environmental variables are shown in Fig. 6. Unlike the clear trends in taxa responses, trait responses are mixed depending on the category and environmental covariate. The exception is bottom temperature, which identifies increasing temperature to have a decreasing effect on the
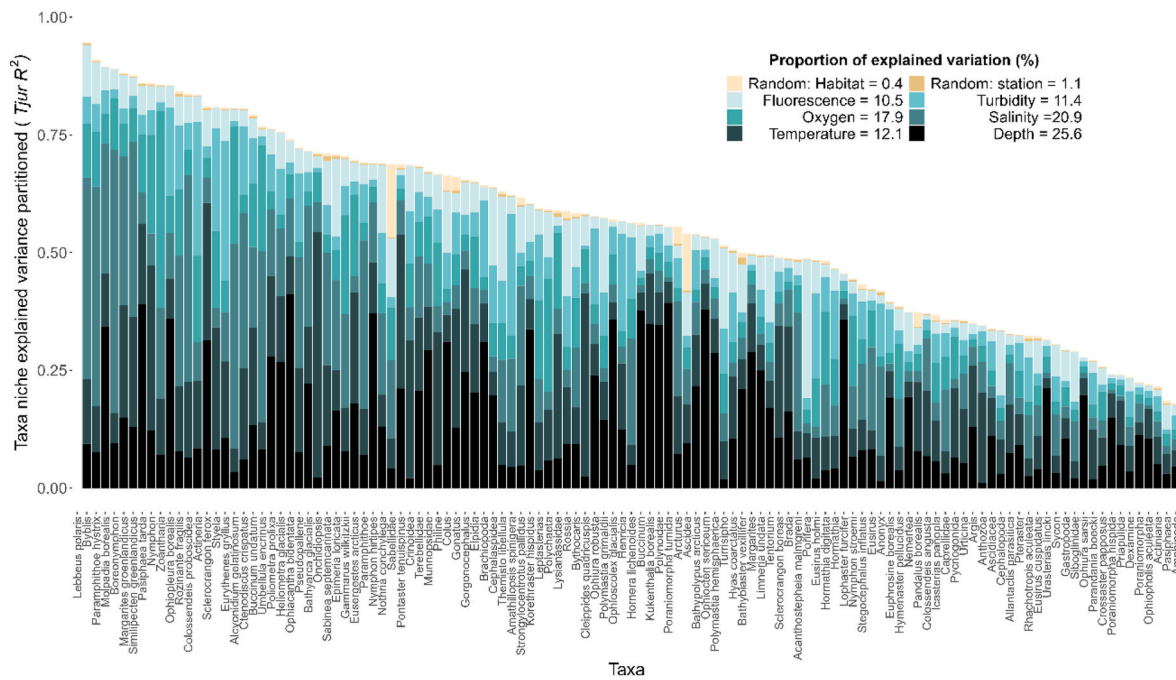
Fig. 5. Total explained variations (*Tjur* R^2) of species occurrences partitioned into responses to fixed (blue coloured bars) and random effects (beige bars). Taxa are ordered by decreasing explanatory power. The bar plot shows species-specific results while the legend indicates the averages of the proportions of the explained variation. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

CWM of some traits (Fig. 6), with no positive effects on any categories at this level of support (posterior probability of 0.9).

4. Discussion

Benthic communities inhabiting continental shelves are influenced by complex physical environments, such as water mass interactions, biogeochemical processes, and biological production of organic matter (Kiesel et al., 2020). While these are known to structure communities across the fjord, shelf, shelf break, and slope of Northeast Greenland (Mayer and Piepenburg, 1996; Sejr et al., 2009; Włodarska-Kowalczuk et al., 2012; Fredriksen et al., 2020), our results highlight, for the first time, distinctions in trait composition between these habitats. Through our analyses, we show (dis)similar groupings of community-weighted trait means (CWM) across each habitat (Fig. 2b and d), indicating shifts in trait composition across the seascape. Furthermore, when investigating the individual traits and their categories, the gradual shifts in trait categories across the habitats (Fig. 3) largely matched our expected distributions (Table 1) for all except body size. Our approach of integrating biological traits with both abundance and biomass data provides complementary information and a greater understanding of the structural and functional diversity of marine benthic invertebrates across the Northeast Greenland habitats. The abundance data provides insights into the distribution and frequency of traits across habitats, revealing gradual shifts in trait expression such as body size and feeding habits. On the other hand, the biomass data emphasizes the ecological weight and significance of these traits, highlighting differences in the proportion of traits like globulose body form and siliceous skeletons. This dual perspective allows for a more comprehensive interpretation of the ecological patterns and processes shaping these communities. We further discuss how environmental filtering and the structural complexity of the seascape (e.g., banks, sills, and troughs) contribute to the observed differences in trait composition, influencing both taxa occurrence and resource use strategies. This supports the presence of divergent trait categories across continental shelf habitats.

An interesting finding of our study regarding the environmental drivers of species occurrence or traits was that temperature was not a main driver, despite the gradient of temperature across the four habitats and the notion that polar taxa have narrow temperature tolerance ranges and are therefore more sensitive to change (Pörtner et al., 2014; Morley et al., 2019; Renaud et al., 2019). Our analysis revealed higher concentrations of oxygen and salinity to positively increase taxa occurrence by 47.5% and 23%, respectively (Fig. 6). The fjord and shelf habitats were the lowest in salinity and highest in oxygen concentrations (with the opposite found on the slope), which was reflected in our results from the HMSC analysis, highlighting water depth, salinity, and oxygen to contribute 64% of the explained variation in taxa occurrences, while only 12% of the explained variance was linked to bottom water temperature. Although Northeast Greenland's seafloor topology and hydrology have been poorly mapped until recently (Arndt et al., 2015; Gjelstrup et al., 2022), they may aid in explaining the environmental structure and taxa occurrence patterns. Gjelstrup et al. (2022) describe a general structure of water masses on the Northeast Greenland Shelf that includes a fresh, local surface layer (<50 m), followed by an intermediate layer of Polar Water with central Arctic origins, and finally, a deep layer of Atlantic Water which is warmer and higher in salinity. The strength of the layering (or stratification) depends on the latitude, time of year, and depth, while the bathymetry, troughs, and sills across the shelf will determine whether the bottom Atlantic Water layer will enter the shallow areas of the shelf or the fjord. Stations in the fjord and shallow shelf are characterised by cold, fresh water with high oxygen content, indicating mixing between the fresh, local layer from ice melt and Polar Water, while the deeper stations with higher salinity, lower oxygen and increased bottom temperatures are plausible to be Atlantic Waters. Thus, the layering of water masses would be the source of biogeochemical variability within and between habitats and could explain why differences in oxygen, salinity, fluorescence, and turbidity structure the epibenthic communities.

Additionally, we predicted that the fjord would have larger taxa due to colder temperatures, yet we found the fjord habitat to have the largest contribution of small–medium taxa. This further challenges the common conception that temperature is the leading driver in community distributions but rather insinuates that it is an indirect driver combined with more prevalent processes on the Northeast Greenland continental shelf
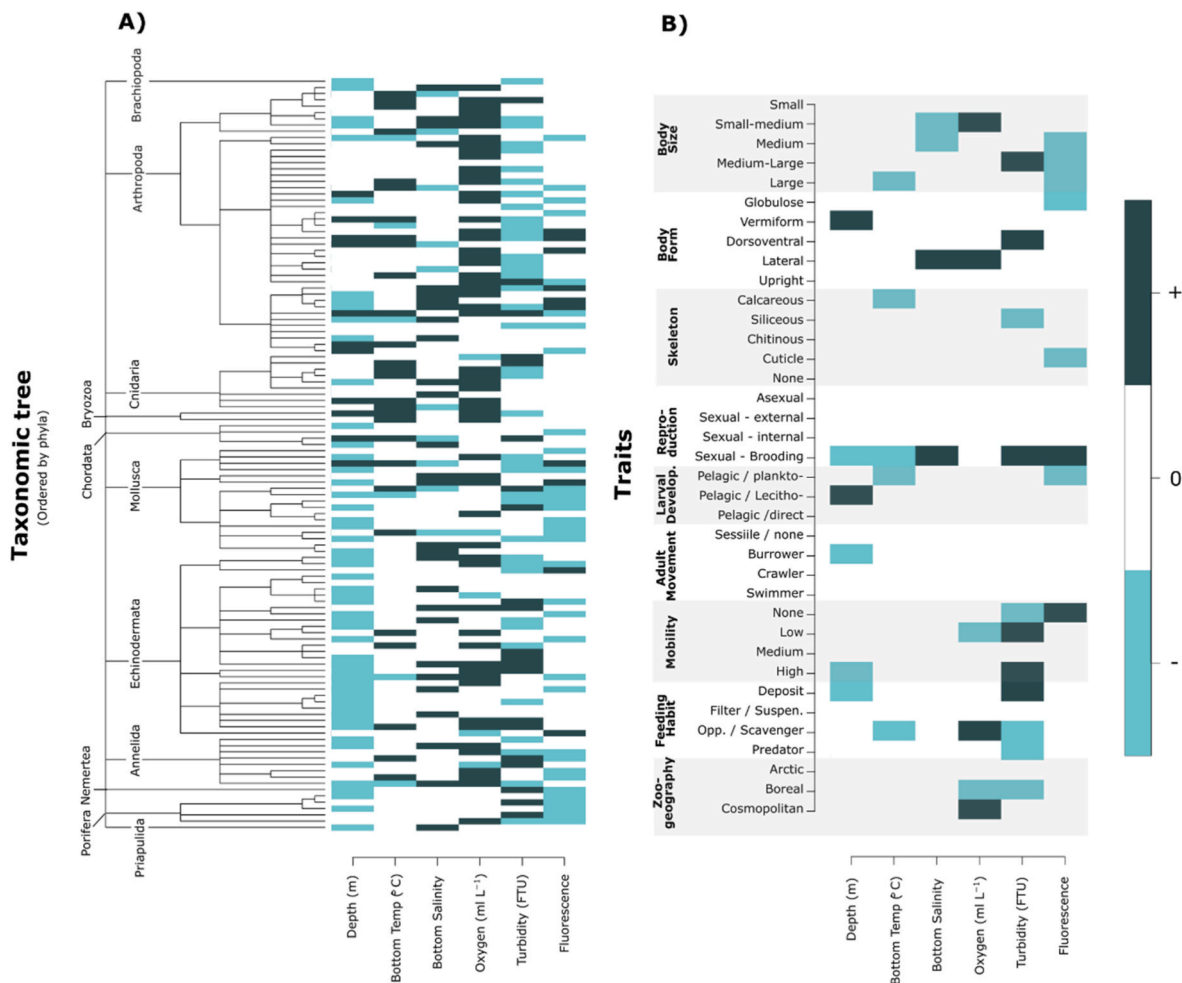
Fig. 6. Linear relationships of A) taxa responses to the environment and B) trait responses to the environment. For A), taxa are ordered according to their taxonomy and illustrated as a taxonomic tree. Phyla names are included at the branch root. In A) and B), taxa and trait responses are shown as positive (dark blue) or negative (light blue) with a posterior probability of 0.9. White responses have no strong significant support. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2

The contribution of traits among responses of Northeast Greenland benthic taxa occurrences to environmental covariates. The explanatory power of traits is expressed as R^2, where 0 has no explanatory power and 1 is fully explained.

Proportion of explained variation in taxa responses to the environment mediated by traits	
Depth (m)	0.50
Bottom Temperature	0.39
Bottom Salinity	0.60
Oxygen	0.75
Turbidity	0.60
Fluorescence	0.57
Proportion of explained variation of taxa occurrences attributed to traits	
Traits	0.53

for benthic assemblages and their ecological functions. For example, Górska and Wlodarska-Kowalczuk (2017) state that the steep environmental gradients (*e.g.,* increasing depth) and increased disturbance from melting glaciers and sea ice (*e.g.,* the introduction of fresh, cool water and glacial debris) in Arctic fjords controls benthic biomass and can shift the community from larger to smaller benthos even with high food availability. Additionally, not all fjords or shelves have the same water depth and sill structure, which modifies water mixing and is responsible for varying concentrations of organic material by marine and terrestrial

inputs, ultimately leading to various benthic compositions with different functional feeding types (Kokarev et al., 2021; Kiesel et al., 2020). Sills within fjords, combined with whether glaciers are marine or land-based terminating, vary in their water mass mixing resulting in some which have stagnated bottom water and high marine deposits (as described in Kokarev et al., 2021), compared to those with high water mixing and environmental disturbance. The latter leads to high species turnover and a diverse assemblage of traits within a relatively small area (Sejr et al., 2000; Górska and Wlodarska-Kowalczuk, 2017), explaining the highly diversified taxa with divergent ecological roles found in this study. Building on the concepts discussed in the preceding paragraphs, we recommend that future researchers expand on our snapshot-in-time analysis by incorporating seafloor boundary currents, pelagic water masses in Arctic environments, and vertical fluxes of particles and organic material into benthic invertebrate studies of the high Arctic. While Gjelstrup et al. (2022) highlight the strengthening of Atlantic water on the East Greenland shelf over time, the duration and historical impact of such changes on benthic Arctic communities remain unclear. Establishing in-situ time series or experimental gradients across environmental variables, such as temperature, could help identify and better understand these signals and their role in species niches and traits. Interdisciplinary research of this nature represents a crucial next step toward disentangling the environmental processes that our study could not fully address.

The fjord habitat was also characterised by a distinct community of

high taxa and functional diversity, but also relatively high taxa vulnerability and low functional redundancy (Fig. 4). While the high taxa vulnerability combined with low functional redundancy raises a concern regarding the resilience of the fjord benthic communities if taxa are sensitive to changes in environmental filtering (Solan et al., 2004), little is understood of benthic turnover, functional stability, or resilience over the long-term in the high Arctic fjords. Here we anticipated (Table 1) and show epibenthic fjord communities to be characterised as predominantly Arctic in biogeographic affinity and benthic/direct development (*i.e.*, low dispersal capability). In contrast to our expectations, our results show mixed movement behaviour and mobility. Yet the proportion of organisms that are sessile with low mobility that are physiologically constrained to cold, arctic temperatures are said to be some of the most threatened by climate warming (Henson et al., 2017; Logerwell et al., 2022). Their risk of extinction under future climate change scenarios remains uncertain, as many species exhibit greater variability in temperature tolerance ranges than previously assumed, likely influenced by historical fluctuations in Arctic systems (Renaud et al., 2019).

Following historical variability, we found no evidence for related taxa responding similarly to the environment, suggesting ecological divergence among related species. Ecological divergence implies that, despite sharing a common ancestry, species have evolved distinct ecological strategies and preferences in response to environmental conditions. This divergence may be driven by various factors, including adaptation to different niches, competitive interactions, or unique evolutionary trajectories (MacArthur and Levins, 1967; Díaz et al., 2013). The absence of similar responses to the environment among related taxa indicates the influence of diverse ecological pressures, such as habitat and the physicochemical properties of the water column, shaping their individual adaptive strategies and making predictions of their resilience to climate change even more difficult to attain.

The slope and shelf-break habitats are dynamic environments where the Return Atlantic Current and East Greenland Current meet and therefore undergo rapid hydrographic modifications from eddy activity and strong advection (Sejr et al., 2017; Gjelstrup et al., 2022). Gradients in biological communities at Arctic shelf breaks and slopes are discussed in detail in Bluhm et al. (2020), but generally, there is enhanced abundance and biomass of zooplankton, benthos, and upper trophic level consumer communities found over the inflow Arctic slopes, but decline with depth due to the diminishing vertical flux of particulate organic matter (Bluhm et al., 2020; Vedenin et al., 2022). Furthermore, taxonomic shifts commonly occur to other species or families within the same class or phylum rather than to entirely different organisms at phyla or class level (Bluhm et al., 2020). This mirrors the findings in our analysis, with significantly higher taxonomic richness and diversity on the shelf compared to the slope where it declines. The functionality of the species is also reflective of the environment across the seascape. On Svalbard slopes, where boundary currents vary from slow-moving to high-flow through speeds and structure bottom sediments, soft-bottom areas host dense populations of deepwater shrimps, while interspersed hard-bottom regions are predominantly inhabited by suspension-feeding *Geodia* sponges (Bluhm et al., 2020; Jørgensen et al., 2022). Crinoidea and Porifera are filter-feeders which require a hard substrate to attach to and were found in high abundance on the shelf break in this study. Mirroring other studies this would indicate strong boundary currents along the slope (Bluhm et al., 2020; Jørgensen et al., 2022).

We also hypothesised that the Return Atlantic Current would explain a higher contribution of cosmopolitan taxa on the slope (Table 1) and found via the biogeography trait that the observed increase in the fraction of cosmopolitan species in the community in the fjord to shelf break areas compared to the slope was considerable (from <20% to >50% of the community composition). Many of the cosmopolitan taxa in our dataset (*e.g.,* arthropods, *Lebbeus polaris, Eusirus* sp., and *Eurythenes gryllus*, and cephalopod, *Gonatus* sp.) are common and indicative of deep ocean habitats where food availability is scarce (Bluhm et al., 2020). While the arm hook squid, *Gonatus fabricii*, is common in deep areas of the North Atlantic, Snoeijs-Leijonmalm et al. (2022) recently found *Gonatus fabricii* to be more common in the central Arctic Ocean than previously thought, where it can be found in the deep scattering layer (100–600 m) and in the shelf break and slopes habitats of our study. As our data provide a snapshot in time rather than a continuous series, it is difficult to detect any northward migrations, particularly those connected to climate change. Historical data have already shown species, such as the Atlantic cod, *Gadus morhua*, and the boreal deep-water shrimp, *Pandalus borealis* (found in this study's datasets) to have migrated from the Atlantic and Barents Sea via the Western Spitzbergen and Return Atlantic currents to the Northeast Greenland area (Drinkwater, 2009; Christiansen et al., 2016), along with other fish and benthic species having range expansions with climate warming across polar shelves (Renaud et al., 2008; Andrews et al., 2019). This is crucial for documenting Arctic species taxonomically and via their biological traits, for comparisons between now and in the future, highlighting the value of studies like this one as a baseline for both biodiversity and trait inventories. Such baselines are essential for developing ecological functioning models that can inform future ecological management.

Traits are increasingly being incorporated into environmental monitoring programmes, and often, an increase in functional diversity is interpreted as being positive for ecosystem health and a target for conservation. However, this is not always the case. Species with range expansions have been shown to increase functional dispersion by adding novel boreal traits in Arctic regions. Frainer et al. (2021), for example, highlight traits that were previously not present in fish assemblages in the Barents Sea. Also, the highly competitive invasive snow crab, now present in the Arctic Barents Sea, threatens native species while redistributing the functional composition (Jørgensen et al., 2019). While these examples show how species range expansions have an impact on ecological functioning, the nine traits (38 categories) used in this present study accounted for a considerable amount of explained variation for taxa occurrences and for community responses to each environmental covariate (Table 2). This finding signifies traits as having an important role in forming and/or maintaining community composition across the continental shelf. While the HMSC results and interpretations from our study are insightful for explaining benthic invertebrate communities, caution is warranted when applying and predicting these outputs to unsampled sites or under new environmental conditions, as seen in our low predictive power following the cross-validation procedure (SM Fig. 10.2). While the method as such has the potential to make powerful community predictions in unsampled areas (e.g. Murillo et al., 2024), the unsatisfactory predictive power in our case was likely due to the limited number of samples and spatial replication of our data. While potential missing covariates may have also played a role, our random effects captured very limited variation in species occurrences beyond the explanatory variables of the fixed effects. We acknowledge that unmeasured environmental covariates or alternative model specifications could still influence species distributions. Furthermore, the use of presence-absence data, which lacks the nuanced complexity of abundance data, often reduces statistical sensitivity to environmental gradients and may underrepresent community dynamics, leading to more cautious conclusions. While there is also a limit to the ecological conclusions we can draw from categorical traits used in this study, it highlights the complexity of climate change, species distributions, and how species behaviour ultimately impacts community assembly processes and therefore ecosystem functioning and ecosystem services. With evidence of Atlantic Water on the Northeast Greenland shelf and fjords (Gjelstrup et al., 2022), it prompts the question of how much traits play a role in benthic resilience to climate change. Hence, future monitoring of the Northeast Greenland shelf, should include the addition of novel traits or a change in trait composition to be used as indicators of ecological tipping cascades that ultimately affect ecosystem

functioning and services (Kortsch et al., 2012).

5. Conclusions

Undoubtedly, the demand to understand local, regional, and wide-scale effects of climate change on species communities and ecosystems in the Arctic is increasing. Yet, while we gather ecological information at the foundational level, interpreting these findings along with the indirect effects of climate change remains a challenge. Here, we presented the first inventory of epifauna invertebrate traits and their diverging categories across the marine continental shelf of Northeast Greenland to aid in deciphering Arctic ecosystem functioning and its connections to the environment. Our results show temperature to be less significant in shaping Arctic benthic communities in both taxonomic and trait distributions (*e.g.,* body size) than the other environmental covariates and their variability, such as salinity, oxygen and depth, across the Northeast Greenland continental shelf. While increasing global temperatures are undoubtedly the reason for changes to the physiochemical structure of the shelf area (*e.g.,* melting glaciers and sea ice causing increased turbidity, water stratification, Atlantification, Borealisation, etc.), our study highlights other environmental factors which often get overlooked in climate change studies. Here we emphasise the interplay of the behaviour of the species themselves (*i.e.,* traits) with environmental covariates, such as salinity and oxygen, which are shaped from the region's bathymetry and oceanography were more prevalent in shaping epibenthic communities across the habitats. Using this study as a reference can allow future studies to expand on Arctic traits and ecological functioning research by either fine-tuning definitions or quantifying facilitative traits or traits that contribute to ecosystem functioning and their relationships to the changing Arctic (Al-Habahbeh et al., 2020).

CRediT authorship contribution statement

Phoebe Armitage: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Anna Törnroos:** Writing – review & editing, Visualization, Supervision, Methodology, Funding acquisition, Conceptualization. **Rosalyn Fredriksen:** Writing – review & editing, Investigation. **Bodil A. Bluhm:** Writing – review & editing, Investigation. **Benjamin Weigel:** Writing – review & editing, Methodology, Formal analysis. **Erik Bonsdorff:** Writing – review & editing, Supervision, Investigation. **Jørgen S. Christiansen:** Writing – review & editing, Investigation. **Marie C. Nordström:** Writing – review & editing, Visualization, Supervision, Investigation, Conceptualization.

Declaration statement

I, Phoebe Armitage (as the corresponding author), can declare that there are no potential conflicts of interest and confirm that this manuscript has not been published elsewhere and is not under consideration by another journal. All co-authors have approved the manuscript and agree with its submission to *Estuarine, Coastal, and Shelf Science.*

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2024.109086.

Data availability

The primary data, along with any sub-data generated from analyses associated with this study, are openly available and accessible. The primary data contains epibenthos abundance, biomass, trait, and environmental information from the TUNU cruises and is available at Zenodo (https://zenodo.org/records/10716116). A GitHub repository contains the main data in the form of an R file along with additional datasets, sub-data created from analyses, and R code used for performing the analyses and generating figures (https://github.com/Phoebe-AA/NE-Greenland-Epibenthos-Trait-Analysis-TUNU-2024).

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