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Research article

Towards a regional baseline of Greenland's continental shelf seabed biodiversity

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ABSTRACT

Polar ecosystems are on the forefront of climate change, yet large parts of our polar seas remain unexplored. This affects our ability to detect change in these regions and hampers global science driven conservation efforts. In Greenland, which is heavily reliant on demersal fisheries, this also affects the economy by complicating sustainability certification. Based on a 8-year benthic bycatch monitoring programme recording primarily megabenthos (>1 cm), we provide a first baseline of the benthic ecosystem in Greenland. We calculated richness, rarity, vulnerable marine ecosystem indicator taxon richness (VME) and biomass across 21 % of the Greenlandic EEZ and suggest seven areas to be considered for management effort based on the 75th percentile of sample distribution for richness, rarity and VMEs. We could identify a clear pattern between East and West Greenland primarily driven by a greater abundance of ostur sponges in the East and greater richness and presence of rare species in the West. We identified patterns of geographic-scale richness (Gamma richness) across depth, latitude, distance from coast and temperature and found that richness decreased with latitude and depth and increased towards the shelf-break as expected. Some deviation from these patterns might have been due to sampling bias. Generally, taxa were found to occupy large spatial regions with few endemic or rare species across the study region. This study is the largest assessment of the benthic Greenlandic shelf ecosystem to date and offers essential guidance to policymakers across the Arctic by providing key knowledge on a hitherto understudied area in the Arctic and implementing an easily applicable approach to conservation area selection that is achievable by nations with limited resources.

1. Introduction

The majority of the Arctic region (as defined by the Council of Arctic Fauna and Flora - CAFF) is ocean, most of which is continental shelf, inhabited by approximately 3000 mega- and macrobenthic species (Piepenburg et al., 2024, https://critterbase.awi.de/panabio). Most benthos in both polar regions are poorly known yet may be comprised of many rarities, endemics, bioconstructors and indicators of vulnerable marine environments (e.g. see https://www.vliz.be/projects/scarmarbin/). With the possible exception of the Barents and Chukchi seas, the organisation, interactions and ecosystem services of benthos within assemblages and communities in polar regions has been little characterised (Ramirez-Llodra et al., 2024). Thus, within high latitude regions, a large scale understanding of ecosystems and their drivers is lacking (Jørgensen et al., 2017; Rogers et al., 2020). This hampers the identification of important and vulnerable systems for protection as well as understand and trace change when it is occurring (Sukhotin and Berger, 2013). Seas within both polar regions are amongst the most and least changing by climate-forcing to date (see Constable, 2022). Large parts of the Arctic Ocean and the West-Antarctic Peninsula, for example, are warming rapidly, whilst East Antarctica and North Greenland have experienced less change (Reeh et al., 2001; Turner and Comiso, 2017; Constable, 2022).

Until recently the East Antarctic and Greenland's seas have been the last refuge of high polar conditions and, unlike anywhere else on Earth, there is no cooler climate envelope for their biota to migrate to (Alabia

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et al., 2018; Logerwell et al., 2022). Both regions are amongst the least well known and understood in terms of ecosystem status, dynamics and climate responses but probably contain many unique and vulnerable elements (Brandt et al., 2007; Bluhm et al., 2011b). To best prioritise the protection of the most important areas to mitigate current nature loss and address the climate change crises it is critical to establish a robust and meaningful biodiversity baseline (Pörtner et al., 2023).

Greenland's seafloor ecosystem is of particular interest as its seas span wide environmental variation with a large latitudinal gradient from temperate to arctic (59°N - 82°N) and a pronounced difference in the water masses influencing East and West. While still offering habitats seemingly little impacted by direct and indirect anthropogenic activities, Greenland's high arctic systems are also starting to be affected by climate change, with sea-ice rapidly decreasing within the last two decades and an observed thinning of cold water mass layers (de Steur et al., 2023; Gjelstrup et al., 2022). Establishing a baseline for the seafloor ecosystem would allow us to better monitor change that will occur in the future but also to understand how other arctic systems that have already been altered significantly, might once have looked. The paradigm of northern hemisphere latitudinal cline in richness across taxa decreasing from subtropics to polar often includes the impression of Greenland inclusion but without the supporting sampling there (see uncertainties in Kaiser et al., 2020, p 20). The lack of global understanding of arctic systems is particularly highlighted by the data paucity available within this region. For example, only 302 benthic taxa present in Greenland are recorded in WORMS (World Register of Marine Species [WoRMS Editorial Board, 2025]), which strongly contrasts with the 9400 taxa found across all of Greenland and the 875 marine taxa recorded in local databases (see also Alfaro-Lucas et al., 2023).

With less than 5.3 % of the Arctic ocean protected (Barry et al., 2023), this lack of knowledge is not an uncommon occurrence for economically weaker states in the Arctic. Whilst extensive mapping and monitoring programmes in Canada, the US and Norway have recorded great species richness across the Arctic (Alfaro-Lucas et al., 2023), smaller nations such as the Faroe Islands, Iceland and Greenland have only recently started to include the status of the seafloor into their surveying activities (Jørgensen et al., 2017). Economical interest such as MSC certification of demersal fisheries (Long and Jones, 2021) is often the strongest motivator for this developing interest in the seafloor ecosystem. This means that, in terms of knowledge on their benthic systems, these regions are far behind while also having limited resources available to dedicate to such surveys. Economic needs and mounting pressure to meaningfully protect 30 % of [nature in] the sea by 2030 requires a better understanding of these underrepresented seafloor areas (Naalakkersuisut, 2021). Therefore, Greenland like other nations introduced a benthic bycatch monitoring project as part of annual fishery stock assessment cruises (Blicher and Arboe, 2017). This project required benthic epifauna caught as part of the stock surveys to be retained, measured, expert-identified and recorded. Whilst not ideal, such surveys have provided a valuable dataset giving a first idea of the current status of the Greenlandic seafloor mega- and macrobiota.

There are very many ways in which the variety of life, biodiversity, can be measured and metricised to aid marine spatial planning. Typically, these include assessments of richness, rarity, endemicity, endangerment and specific terms such as 'Vulnerable Marine Ecosystem' indicators (Carwardine et al., 2009; Ardron et al., 2014; Harris and Holness, 2023). A key purpose of designation and implementation of nature protection is to effect change by actually mitigating threat. Thus, the distribution, intensity and trend of potential threats also needs to be considered. Consideration of the geography, trajectory and interactions between potential threats is critical to assessments and efficacy of action.

For Greenland's coast and continental shelf, we see priorities of establishing a seabed biology knowledge baseline across spatial scales and biological criteria, which is the goal of the current work. With a strongly fjordic coast, marine terminating glaciers and much seasonal marine ice there are likely to be many emergent environments and a rich Arctic biota of high value to global biodiversity and ecosystem services such as marine carbon pathways to sequestration. Here, we aim to identify particularly important areas for benthic megafauna within Greenland's EEZ which could be integrated into the budding management approach by the Greenlandic government by providing a first comprehensive understanding of species richness distribution across the Greenlandic Shelf, identify important areas for vulnerable marine ecosystem indicators and rare species and assess broad scale diversity patterns.

2. Methods

2.1. Study area

The study area (Fig. 1) encompassed 473 thousand km^{2}of SE, S, SW, and W-Greenland. It covered approximately 36 % of Greenland's continental shelf and 21 % of its 2.27 million km^2 EEZ. Sample effort was not equal across regions, with distance from coast or bathymetry (Fig. 2a).

Greatest efforts have been made around the SE-shelf edge, and to a lesser extent towards the East and West shelf edges. Demersal fishing effort was also very unequal across Greenland, with much effort focussed within relatively small areas of Greenland's East and West shelf edge (Fig. 2b).

2.2. Data collection

Data was collected between 2015 and 2023 as part of Greenland's fishery stock assessment cruises and specific dedicated sampling campaigns (Yesson et al., 2015; Gougeon et al., 2017; Long et al., 2020; Krawczyk et al., 2021). Stations for the fisheries stock assessment are chosen randomly across the areas primarily targeted for fishing (Fig. 2), stations for dedicated sampling campaign were chosen randomly or based on the specific objective of the campaign in the target region (Yesson et al., 2015; Long et al., 2020; Krawczyk et al., 2021, 2024). Sampling effort differed between years owing to logistical constraints (SFig. 1). Epi-zoobenthic bycatch from demersal trawls was collected, weighed (wet mass) and identified to the lowest taxonomic resolution possible by benthic taxonomists. Some specimens, such as unknown individuals of the phylum porifera could only be grouped into morphotype (e.g. vase-shaped, or branching). Trawls were carried out using several different gear-types dependent on target species and area. Beam trawls for specific benthic surveys were towed for ~6 min at various depths spanning 50–1500 m, Cosmos Trawls focusing on shrimp and cod assessments were towed for ~15 min across shelf habitats (50–600 m), and Alfredo trawls, targeted at Halibut were pulled for ~30 min along the shelf break and within deep troughs along the shelf (400–1500 m). Thus, the majority of invertebrates collected represented megafauna (>1 cm), with a lower proportion of macrofauna (250 μm–1 cm) also present in the dataset. To avoid potential confounding effect of different gear types, analysis was restricted to richness and analysis of biomass was restricted to samples from cosmos trawls, as they represented the greatest number of samples across the widest area. A total of 2916 stations or 48,446 individual taxa observations were included in this dataset. Depth and temperature at the bottom was noted at the start and end of each transect and a mean was calculated for each. Swept area of each trawl was calculated in m^2 by multiplying trawled distance with width of the door spread.

2.3. Data preparation

The resulting dataset was quality controlled and cleaned of any pelagic species. Cnidarians with a benthic and pelagic lifecycle were removed from the dataset as primarily the pelagic life stages (e.g. Medusa) had been recorded during data collection. Owing to sensitivity

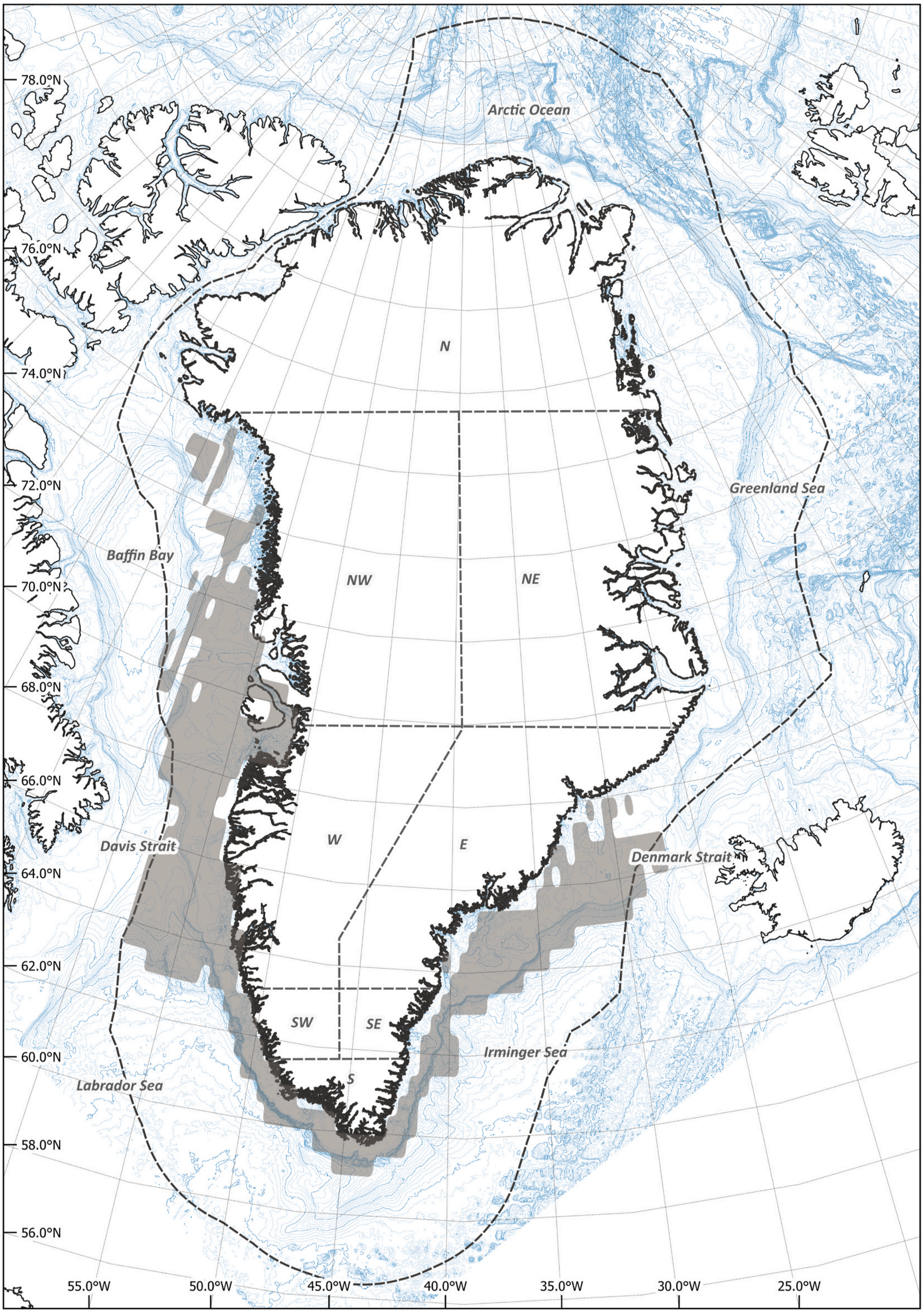

Fig. 1. Greenland and its surrounding seas. The shaded area highlights the study area, The dashed line represents the Greenland EEZ. Letters denote broad geographical regions referred to in the manuscript. Bathymetry has been sourced from IBCAO (Jakobsson et al., 2020).

around the distribution of commercially harvested species in Greenland, such as the shrimp *Pandalus borealis*, these were not included in the analysis. To avoid an artificial inflation of species richness, 49 occurrences of taxa that only appeared once, and were recorded at a taxonomic level of class, order or family, were removed from the dataset if other taxa from the same taxonomic level, but identified to a lower taxonomic resolution, were present. The midpoint of each trawl was calculated and used for spatial analysis. Wet mass was standardised to m^2 of the swept area. Identification and selection of Vulnerable Marine Ecosystem Indicator taxa was based on the FAO VME indicator list for the NorthWest Atlantic and the NorthEast Atlantic (FAO, 2024). Thus, we collated occurrence data for corals, specifically the orders Pennatulacea, Scleractinia, Antipatharia, the families Capnellidae, Gorgoniidae and the genus *Gersemi,* for sponges, the class: Hexactinellida, and order Tetractinellida, for featherstars the class Crinoidea, and for Bryozoans the genus *Reteporella* and *Hornera* as representative VME indicator taxa.

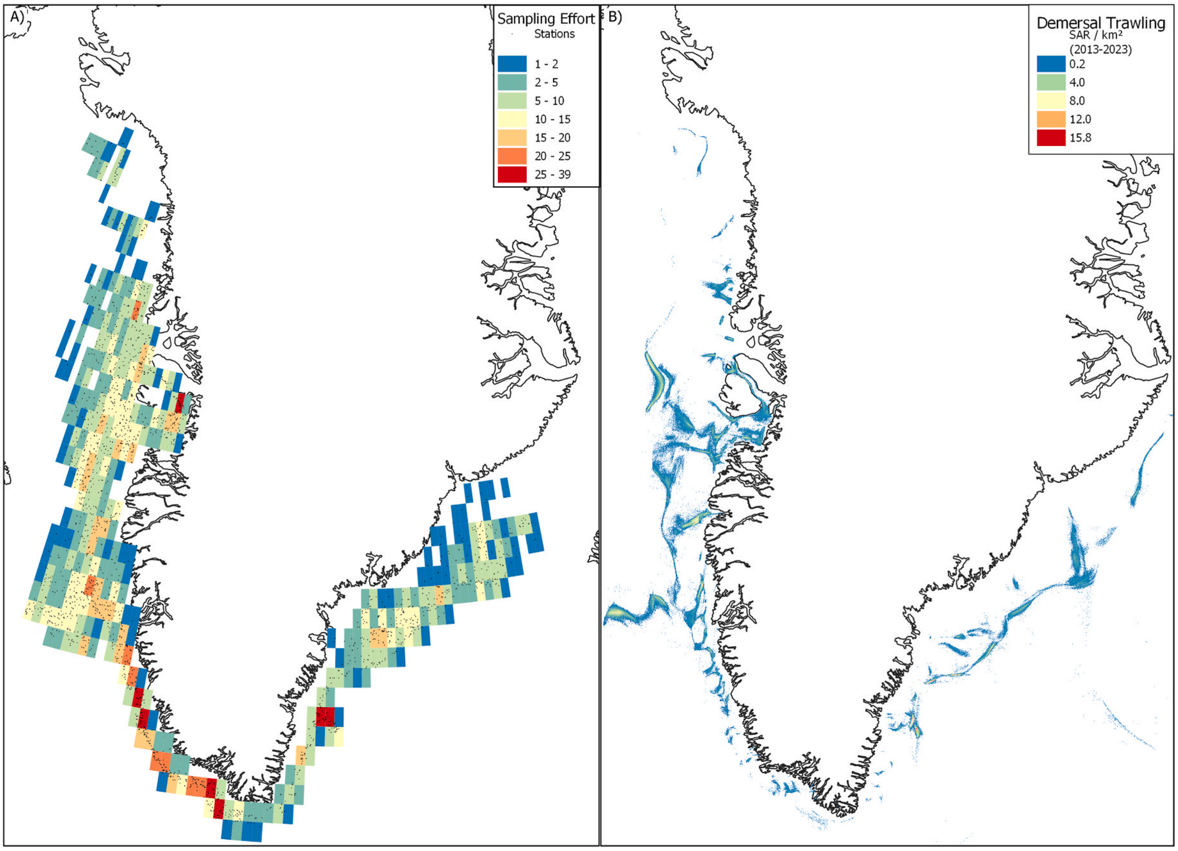

Fig. 2. Sampling effort or stations per gridcell (A) and swept area ratio (SAR)/km^2 for mobile bottom gear between 2013 and 2023 (B) within Greenland. Grid cells represent 0.5°^{2}. Higher sampling or fishing effort is represented by warmer colours. Small black dots represent the mid position of the actual sample.

Rare taxa were those identified as occurring in the dataset 3 times or less which constituted 1.1 % of all observations (Gaston, 1994).

Wet mass to ash free dry mass (AFDM) conversion rates were obtained for relevant VME taxa for Hexactinellida, Crinoidea, Tetractinellida, Capnellidae, *Reteporella* and *Hornera* during a cruise in E-Greenland in August 2023. Conversion rates for Capnellidae were applied to *Gersemia* as both represent soft corals with a similar growth form (Behrisch, 2025). Wet mass for 5 to 35 individuals of each taxa were estimated upon collection. Individuals were then dried for at least 48 h at 70 °C until they had reached constant mass and were subsequently burned for 24 h at 480 °C. Conversion rates were calculated based on the slope of linear regressions between wet mass and AFDM (Behrisch, 2025). R^2 values of conversion rates for these taxa were generally larger than 0.80, indicating that WM is a good predictor for AFDM (Behrisch, 2025). Owing to the fact that no conversion rates for hard coral families could be obtained these were not included in the figures representing AFDM.

For richness analysis two datasets were created, one including all observations at the lowest identified taxonomic resolution, including morphotaxa (hereafter referred to as taxon richness) and one at a family or higher taxonomic resolution (hereafter referred to as family richness)

2.4. Spatial analysis

Spatial layers were created for sampling effort (number of stations per grid cell), taxon and family richness, standardised taxon and family richness (richness hotspots), biomass (g/m^2 wet mass from cosmos trawls), rare taxon richness (defined as three or less total records across the complete dataset), VME taxon richness and biomass with 1°, 0.5° and 0.25° resolution in QGIS 3.26 using a EPSG: 4326 projection. Area calculation, however was based on EPSG 3413 NSIDC Sea Ice Polar Stereographic North to better represent the geographic region. It was found that the 0.5° layer best represented the data while allowing to identify pattern of taxon richness across the study area. Overall, rare and VME indicator taxa richness was calculated using the open source FSC biolink plug-in for QGIS. To identify hotspots of richness, residuals of a linear model between richness and effort were extracted and plotted for taxon ($r^2 = 0.6$, $t_{1,\ 397} = 24.30$, $p < 0.001$) and family richness ($r^2 = 0.55$, $t_{1,\ 401} = 22.13$, $p < 0.001$). As has been shown previously, cosmos and alfredo trawls are biased towards megafauna and only capture a fifth of the richness and an order of magnitude less biomass compared to beam or Agassi trawls, which are more commonly deployed for scientific studies (Blicher and Hammeken Arboe, 2017). To identify whether the comparatively larger effort with cosmos trawls ($n = 2056$) compared to alfredo ($n = 472$) and beamtrawls ($n = 384$) may have negated this effect, an ANOVA was carried out using richness per grid cells as dependent variable and used gear type (factorial, 7 levels: alfredo trawl, beamtrawl, cosmos trawl, alfredo-beamtrawl, alfredo-cosmos trawl, cosmos-beam trawl and alfredo-cosmos-beamtrawl) and total sampling effort (continuous) as explanatory variables. Tukey post-hoc tests with a Bonferroni correction were applied to identify gear types with significantly different richness associated with them.

To explore whether sampling effort was sufficient to capture likely species richness within each grid cell, species accumulation curves based on the clench model were calculated for each 0.5° grid cell using the KnowBR R-package (Guisande Gonzalez and Lobo, 2023). Slope between the last two sampling points was calculated and visualised.

To identify areas of high conservation value, a conservation index was calculated based on composite maps of combined mean values in ArcGIS. Here, input variables were standardised to values between 0 and 1 and a mean calculated across spatial layers for taxon richness, VME richness, rare taxa richness and hotspots (e.g. residuals). A composite confidence layer was also calculated based on the slope of the species accumulation curves and sampling effort. Species accumulation curves were included in the reverse order here, meaning low values e.g. approaching asymptote were given greater values. To test how well such calculated indices represent the original input parameters, linear models were carried out with the composite index as the predictor variable and the original input parameters as the independent variables. Residuals of the model were assessed for normal distribution and homogeneity of variance.

2.5. Richness and taxon distribution

To identify how taxon richness correlated with potential large-scale spatial drivers in Greenland, gamma diversity was assessed against latitude, distance to the shelf break, depth and temperature for both West and E-Greenland. The dataset was split at 42.8° W based on the most southerly point of Greenland. To assess the relationship of richness with latitude (59°–77°), the dataset was restricted to samples collected on the shelf and gamma richness was calculated over 2° bands and standardised to 1000 km^2 areas to account for the significantly narrower shelf regions in S-Greenland. Distance to shelf break was extracted for each sampling station from a shelf break polygon based on available IBCAO bathymetry data (Jakobsson et al., 2020). Percentage distance of each sampling station to the shore was calculated with the shelf break representing 100 % distance from coast. This means sampling stations on the shelf slope have a distance greater than 100 % (0 %–140 %). Gamma richness with shelf distance was calculated within 5 % increments. Gamma richness was calculated for 100 m depth intervals (0–1500 m), with the exception of the 0–100 m interval which was split into two 50 m intervals to better differentiate between shallow and deep-sea taxa richness. To understand how richness responds to changes in sea-floor temperature, the observed temperature gradient (−1.7 °C to +8.8 °C) was split into 1 °C intervals for each of which gamma richness was calculated.

To better understand species dynamics across Greenland we calculated distributional ranges of each family for latitude, distance to shelf edge, depth and sea-floor temperature based on the median occurrence of each within the dataset. To further shed light on the size of environmental niches occupied by taxa in West and East Greenland, we calculated the number of all taxa and those identified to species level occupying 0–100 % of the environmental range in 5 % intervals for latitudinal, distance to shelf edge, depth and temperature. Rare taxa and taxa with missing parameters were excluded from this dataset. All non GIS-based analysis were carried out in R version 4.1.3 (R Core Team, 2020).

3. Results

The richness of marine macro- and megabenthos was not evenly distributed around the southern half of Greenland's continental shelf. Total number of taxa reported in this study was 1207 (1136 in West Greenland and 619 in East Greenland), of which 657 (628 in West and 292 in East Greenland) were identified to species level. Most taxa were found within the first 4 years of surveying. However, 10 years later a new taxon is still being recorded every 10 stations (Fig. S1). Richness extent was patchily distributed (Fig. 3a) but showed a particular concentration on the SW continental shelf edge. Such a pattern was not clear at the family level (Fig. S2a). When standardized for sampling intensity the SW shelf break hotspot was less distinct but areas of high richness still spanned the SW to West (Fig. 3b). This remained true for family level standardized by effort (Fig. S2b). In both cases, the SE to East region contained many of the least rich grid cells.

Richness within grid cells significantly increased with sampling effort ($F_{1,\ 386} = 808.085$; $p < 0.0001$) and was affected by gear type ($F_{6,386} = 24.613$; $p < 0.0001$). Post-hoc test showed that richness was similar between grid cells sampled by only one gear type (mean richness ± SD; alfredo: 32.18 ± 12.03, beamtrawl: 45.64 ± 24.5, cosmos trawl: 41.3 ± 24.17) and those sampled with a combination of alfredo- and beamtrawls (40.68 ± 33.47). Richness in grid cells sampled with one gear type or alfredo and beamtrawls was lower than in grid cells sampled with all three gear types (116.76 ± 59.3) and a combination of cosmos and beamtrawls (98.54 ± 47.56) which were similar to each other. Richness in gridcells sampled with the combination of cosmos and alfredo trawl (73.73 ± 27.001) differed significantly to all other gear types with the exception of those only sampled with beamtrawls. This may indicate that gear type itself does not affect total richness but that high heterogeneity in seabed geomorphology and depth strata within the grid cells sampled with a variety of gear types increased richness.

Biomass showed a largely contrasting geographic pattern with highest values found in the SE to East (Fig. 3c). Although there were some grid cells high or low in both richness and biomass, this was rare. Patches of high biomass on the West were primarily found close to the coast and on the SW shelf edge.

Species accumulation curves showed that areas of the SW-shelf were approaching asymptote, suggesting adequate sampling to detect richness of larger biota (Fig. 3d). In contrast most regions in NW and E-Greenland require further sampling effort to robustly describe benthic communities in these regions.

Within the study area, Echinodermata was the most abundant Phylum (>10,000 observations), followed by Arthropoda, Cnidaria and Porifera (9520, 8085, and 6591 observations respectively). These were also amongst the most speciose Phyla, with Arthropoda including the greatest number of taxa (257). Amongst the Echinodermata, the brittlestar *Ophiopholis aculeata* was particularly abundant (1107 observations), whilst the starfish *Henrica* sp. was high in abundance (853 observations) and biomass (3750 kg) and the sea cucumber *Cucumaria frondosa* greatest in biomass (4290 kg). Porifera represented the phylum with the highest biomass (147,624 kg), which included species such as *Geodia macandrewii, Geodia atlantica*, and *Melonachora elliptica,* which although high in biomass (958, 398, and 5275 kg) were observed less frequently (32,18,105 observation respectively). Yet the genus *Geodia* sp. was observed 417 times. Although comparatively high in observations (3734 observations) and biomass (271 kg), bryozoans only included 85 taxa. Sipuncula and Brachiopoda, on the other hand, were amongst the least speciose (14 and 11 taxa respectively), abundant (318 and 413 observations respectively) and high in biomass (1.7 and 2.6 kg, respectively).

A total of 322 taxa were recorded as rare over 563 observations. Numbers of rare taxa per grid cell were low and patchily distributed across our study area. Greatest numbers of rare taxa were found in W-Greenland, specifically in the SW to West, with distinctly less found in the North. This pattern was even more pronounced when investigating family level rarity (Fig. S2c). 72 families were found to be rare over 103 observations. Many hotspots of rarity overlapped with some of effort-corrected richness (hotspots), raising their potential conservation importance. The majority of rare taxa belonged to the classes Malacostraca (n = 71), Hydrozoa (n = 48), Polychaeta (n = 35), Gastropoda (n = 30) and Gymnolaemata (n = 20). This also includes 7 seapens, some of which have not officially been recorded in Greenland before (according to WORMS) including *Pennatula aculeata,* mostly found in the Gulf of Saint Lawrence, *Ptilella inflata,* so far only recorded in South Africa and the N-Pacific, *Pennatula phosporea*, primarily found around the shelf of Europe and North America, and *Radicipes gracilis* and *Scleroptilum grandiflorum* of which only 125 and 146 occurrences respectively, so far have been registered in WORMS. Whilst it is likely that the observed rarity for larger epifauna is a true representation, rare small taxa such as Polychaeta or Hydrozoa may be underrepresented owing to the selectivity of the sampling gear and expertise of taxonomists. Some hydrozoan species recorded as rare in this study have a notably larger record in WORMS if they are also found in more temperate regions, such as *Setularella gayi* with 3419 records, few of which are in the Arctic.

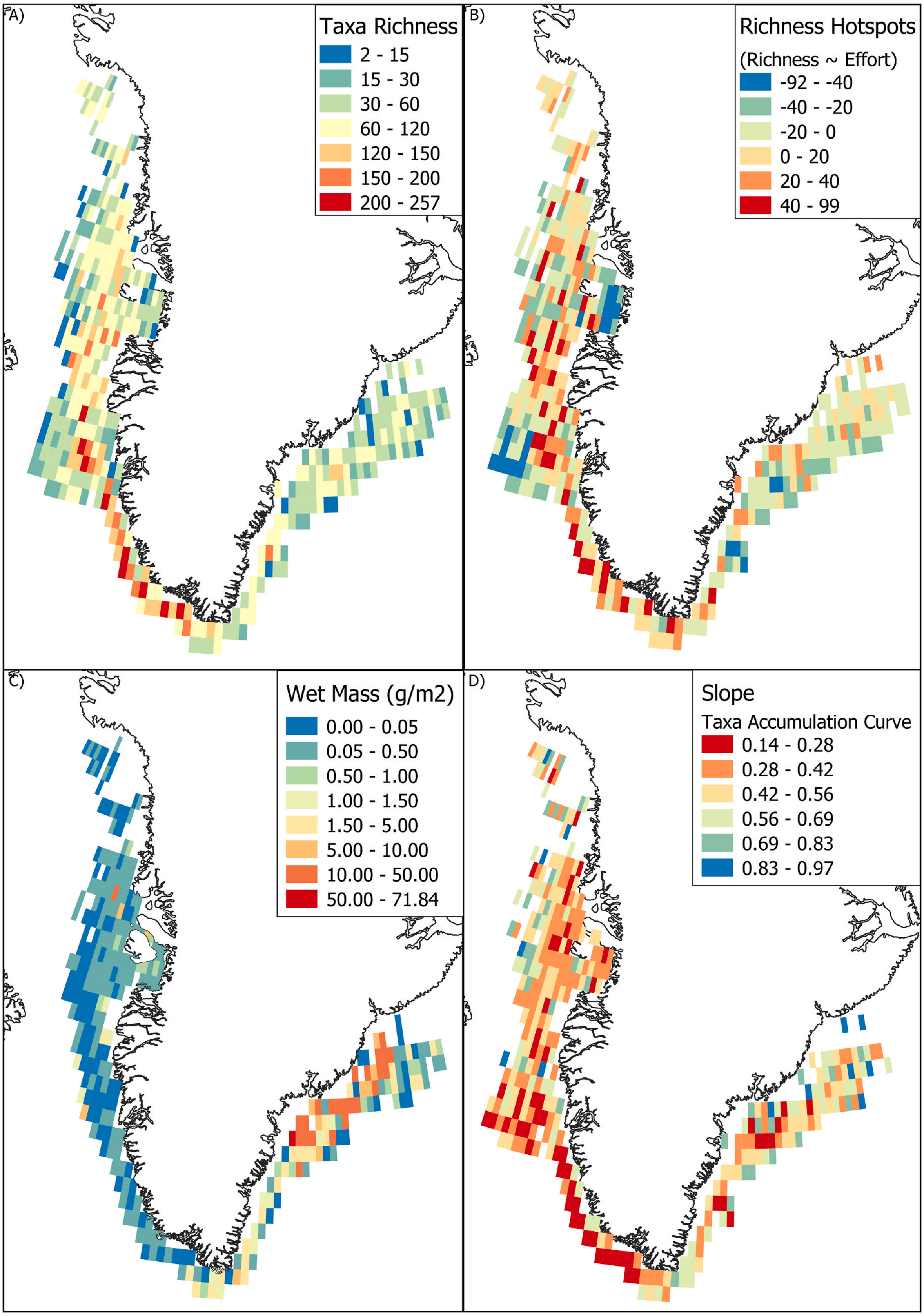

Fig. 3. Distribution of Taxon Richness (A), Hotspots of Taxon Richness (B), Mean Wet Mass/m^2 based on cosmos trawls (C) and final slope of taxa accumulation curves (B) across the sampling area. Grid cells represent 0.5°^{2}. Warmer colours represent higher richness, biomass or the likelihood of sufficient sampling per grid cell. Hotspots of richness were based on the residuals of a linear model between richness and sampling effort, with positive residuals representing hotspots (e.g. greater than expected richness) and negative residuals representing lower than expected richness.

Zygophylax brownie and *Pericladium mirabilis* which are only found in the Arctic have only been found 6 and 51 times respectively.

A total of 77 VME indicator taxa were found across 1831 stations, indicating that over half of all sampled stations contained at least one (Fig. 4b). As with richness and rarity, a most evident pattern for VME indicators was of patchiness. In the West, greatest VME richness (up to 24 taxa) was observed between the Davis strait and the Labrador Sea. High VME richness (8–16) was also found on the continental shelf edge of S-Greenland, with areas containing moderate to high (12–20 taxa) numbers of VME taxa expanding towards E-Greenland. A similar pattern could also be observed for VME families (Fig. S2d). Yet, the only area containing more than 12 VME families was the Davis strait on the West coast. AFDM for VME taxa (without corals) showed the same geographical pattern as overall biomass with high biomass in the East and around the southern tip of Greenland (Fig. 4c). A linear regression model between wet mass of all VME taxa and AFDM of VME taxa without hard corals showed a significant correlation between the two ($T_{1,279} = 6188.79$, $p < 0.001$, $r^2 = 0.99$, Fig. S3).

Larger areas with high conservation value are located in W-Greenland compared to the East. Composite maps especially highlight areas around the shelf slope in SW Greenland, and the Southern and Northern boundary of the Davis Strait (conservation index >0.4) (Fig. 5a). The confidence layer shows that these areas were well sampled with the species accumulation curve approaching asymptote (>0.7). The majority of the study area, however, is still undersampled with a tendency towards better sample coverage and greater confidence in results for W-Greenland (Fig. 5b). Linear models between the conservation index and the input parameters revealed good to moderate fit (R^2) for the different levels of richness (Table 1 a Fig. S9). Linear models for the confidence index, on the other hand, showed a good fit (R^2) for both the slope of the species accumulation curve and the sampling size per grid cell (Table 1 b).

Generally, taxon richness followed similar patterns along broad spatial drivers in West and E-Greenland, yet lower sample size in E-Greenland may have introduced bias. Overall taxon richness strongly decreased with increasing latitude for both East and West Greenland (Fig. 6a). At 76°N on W-Greenland's continental shelf (high Arctic), richness was lower than a quarter of that at 60°N (cool temperate). Broken down by distance relative to the shelf break, we found a distinct onshore-offshore pattern with richness increasing from coast then declining from the shelf break rapidly down the continental slope (Fig. 6b). This pattern was stronger in E-Greenland (Fig. 6b). Such data implies also a richness-depth relationship, which on exploration (Fig. 6c) showed that the steep decline in richness on the upper continental slope reached asymptote by 1000 m. Surprisingly, in W-Greenland the lower slope levels of richness were not dissimilar to those in shallow areas <100 m. In E-Greenland taxon richness was lowest at 1000–1200 m and starts to increase again with further depth. At 1500 m taxon richness was similar in West and E-Greenland. In W-Greenland, taxon richness showed a unimodal distribution along a sea-floor temperature gradient with lower richness at low (−1.5 °C) and high (6.5 °C) temperatures and a maximum between 1.5 °C and 3.5 °C (Fig. 6d). A similar but less pronounced pattern was found for E-Greenland where low richness was also associated with low (−0.5 °C) and high (8.5 °C) temperatures, but taxon richness peaked at slightly warmer temperatures of 3.5–4.5 °C (Fig. 6d).

The distribution of all taxa and species across various spatial drivers is notably more restricted in East Greenland compared to West Greenland (Fig. 7, Fig. S8). In West Greenland, nearly 10 % of all taxa are found across 90 % of the sampled latitudinal range (59°–77°), with some families, such as Elpidiidae, Virgulariidae, and Volutomitridae (Fig. S4), being endemic to higher latitudes. Conversely, East Greenland shows a latitudinal distribution of only 35 % for many taxa, with no sampling above 68°, this is also reflected in the patterns at species level (Fig. 7a, Fig. S8a). In terms of shelf width, over 25 % of taxa in West Greenland cover 70–80 %, while most taxa and species in East Greenland cover less than 60 % (Fig. 7b, Fig. S8b). Only few families have been found that are strictly coastal or limited to the shelf slope (Fig. S5). Depth emerges as a significant factor influencing species distribution; about one-third of taxa or species occupy only 10–40 % of the depth range (Fig. 7c, Fig. S8c), with families like Tethyidae, Edwardsiidae, and Ancorinidae covering larger portions (Fig. S6). Notably, families in shallower waters tend to have more limited depth distributions, although those in East Greenland occupy a broader depth gradient than their West Greenland counterparts. Temperature ranges also affect taxa distribution similarly to distribution of only those identified to species level, with over 25 % covering 50–60 % of the temperature spectrum (Fig. 7d, Fig. S8d). A marked decline occurs for taxa found across broader temperature gradients. Some few families, such as Synopiidae, are exclusively found in subzero waters, while many more occur between −1.7 °C and 5 °C (Fig. S7). Most taxa appear to have an upper temperature limit around 6 °C, with a few families like Thoridae and Solasteridae found with particularly great temperature ranges along the East coast.

4. Discussion

Polar marine ecosystems are on the forefront of the twinned crisis of climate change and biodiversity loss (Pörtner et al., 2023), yet limited knowledge on distribution and functioning of these systems hampers conservation efforts. International commitments to protect 30 % of ocean by 2030 and pressure to synergise nature conservation with climate mitigation (Pörtner et al., 2023), increases the need to provide a better understanding of these ecosystems to aid evidence-based protection. Here, we provide a first circum-southern survey of knowledge of the seafloor ecosystem around Greenland. Although there were strong similarities in benthic assemblages throughout this large region, there was a distinct difference between the East and West coast and great variability with latitude and a gradient from coast to the shelf edge. This is often the case with other locations spanning >20 degrees of latitude with coasts facing multiple seas (e.g. Australia, Canada & USA). Such differences are important for marine spatial planning and meaningful protection. A greater understanding of the location, size, number of areas and their designation features will aid management decisions. For example, the clear differences in community patterns between East and West Greenland, with greater richness and occurrence of rare species associated with the West and greater levels of biomass in the East, may help to aid and inform management here. Large scale spatial patterns help to explain polar sea richness in a global context (Kaiser et al., 2020) but also pinpoint broader areas for management concern, such as the shelf edge. Generally, we found that richness followed a predictable trend not just across latitude, but also with distance from shore and depth, although low sampling effort for East Greenland may have contributed to some unexpected patterns. Interestingly, Greenland benthic taxa did not conform to expectations along a temperature gradient. Generally, we could show that benthic taxa around Greenland seems to be much more generalist than expected in a polar environment.

4.1. *Greenland richness pattern in an Arctic context*

The Greenland EEZ constitutes a large part of the Arctic, yet limited information is available on how the seafloor ecosystem here, compares to other polar regions. We could show that levels of richness for benthic megafauna across large regions of Greenland are similar to those across the Arctic seas, where Arthropoda were also the most speciose phylum (>600 vs 257 in Greenland, with 366 observed in the Arctic Ocean) (Bluhm et al., 2011a, 2011b; Saeedi et al., 2019; Piepenburg et al., 2024; Ramirez-Llodra et al., 2024), yet higher levels of richness were observed for Cnidaria (216 in Greenland vs 61 in the Arctic Ocean and <150 in the Arctic), Mollusca (183 in Greenland vs 70 in the Arctic Ocean and <300 in the Arctic), Echinodermata (158 in Greenland vs 38 in the Arctic Ocean and >150 in the Arctic) and Porifera (100 in Greenland vs 29 in

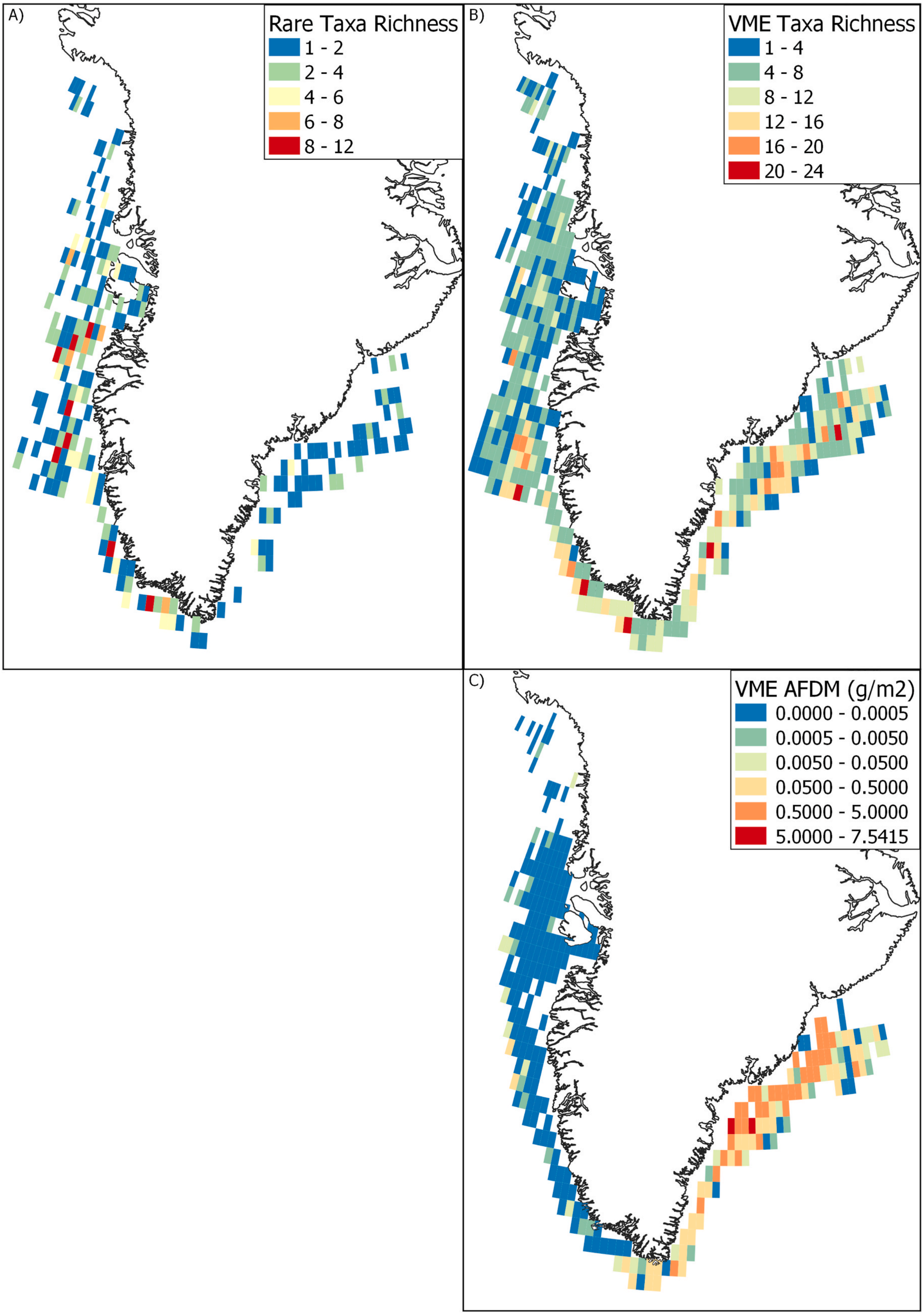

Fig. 4. Distribution of taxon richness for rare Taxa (A), Vulnerable Marine Ecosystem Indicator Taxa (B) and Ash Free Dry Mass (g/m^2) of VME Taxa (C) across the sampling region. Biomass calculations were based on all samples collected with a cosmos trawl. Grid cells represent 0.5$^{\circ 2}$. Warmer colours represent higher richness or biomass.

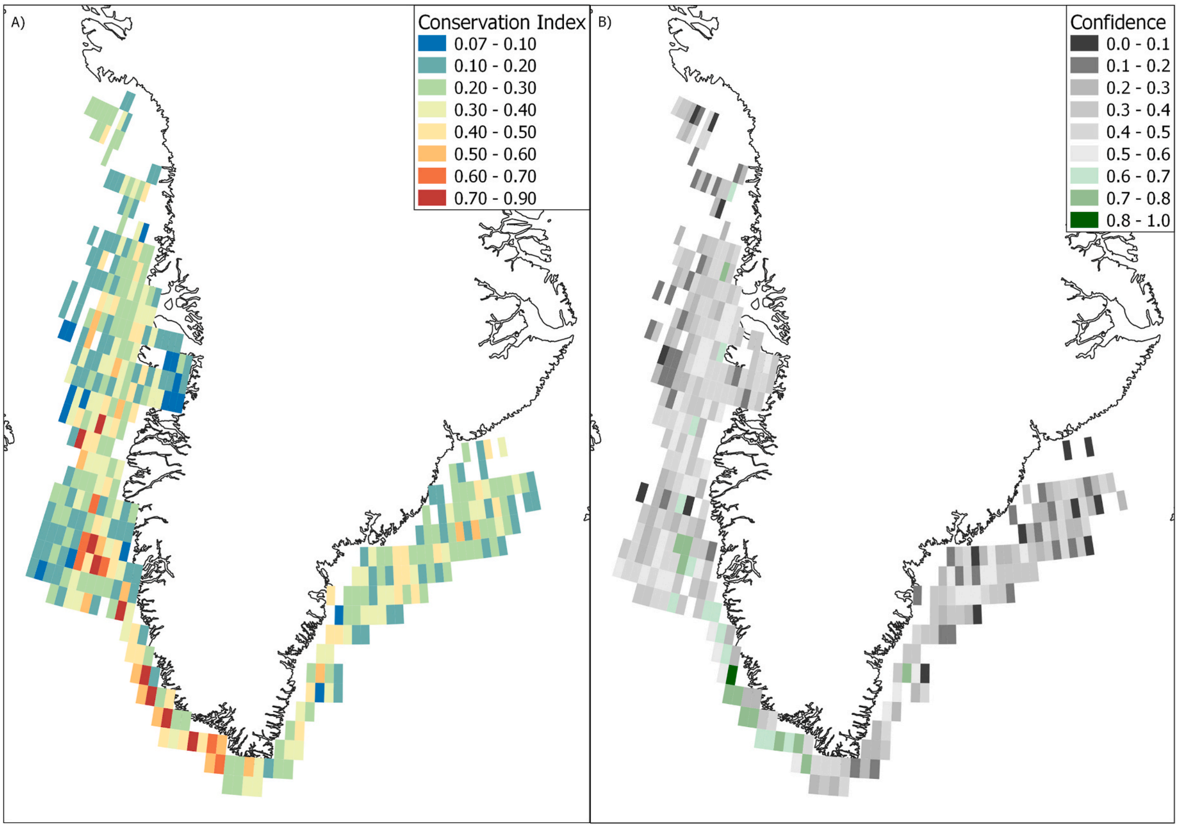

Fig. 5. Potential areas of conservation interest (A) and confidence in accuracy of the conservation index (B). Conservation indices were based on the mean of standardised overall taxon richness and taxon richness for rare and VME indicator taxa as well as richness hotspots. Confidence values were based on the mean of a standardised sampling effort and slope of species accumulation curves. Grid cells represent $0.5^{\circ 2}$. Greater conservation indices are represented in warmer colours. Greater confidence is represented with green grid cells.

Table 1
Regression analysis between A) Conservation Index and B) Confidence Index and explanatory variables.

	DF	F	R^2	P
A) *Conservation Index*				
Taxon Richness	397	2337.0	0.8548	<0.0001
Hotspots (residuals)	397	498.4	0.5566	<0.0001
Rare Taxa Richness	397	610.8	0.6061	<0.0001
VME Taxa Richness	397	538.7	0.5757	<0.0001
B) *Confidence Index*				
Slope	350	3092.0	0.8980	<0.0001
Effort	350	820.7	0.7002	<0.0001

the Arctic Ocean and >100 in the Arctic) in Greenland, possibly owing to the presence of both boreal and truly arctic taxa across Greenland's latitudinal gradient (see https://www.marinespecies.org/arms/for distributions). With large parts of the Greenland EEZ under sampled, it is likely that taxa richness found during this study is still an underrepresentation. In the Barents Sea, which is approximately two-thirds the size of the Greenland EEZ a similar monitoring programme has found a total of 354 taxa within one year (Jørgensen et al., 2015) and 1054 taxa during a 12 year effort covering all of the Barents Sea (Zakharov et al., 2020). Similarly, along the gradient of the Canadian Arctic to the Atlantic, higher levels of taxon richness are expected than have currently been observed (Wei et al., 2020). For some regions with a continuous high sampling effort, such as the Barents Sea current numbers might prove accurate. For Greenland, Bluhm et al.'s (2011b) prediction of a much greater benthic species richness than so far recorded in the Arctic is likely to hold true. Our data shows, for example, that new records of taxa are still being detected every 10 stations within our current sampling range.

Substratum type is a significant structuring force for deep-sea benthos (Hewitt et al., 2005; Young et al., 2022). For instance, around South Georgia's shelf, most biodiversity, epibenthic biomass, and zoobenthic carbon stocks are linked to rocky habitats (e.g. moraines) rather than soft sediments (Barnes and Sands, 2017). In contrast, in the Barents Sea, zoobenthic variability was as great between habitat and substratum types as within it (Souster et al., 2024). Unfortunately, comprehensive substratum maps for Greenland are lacking, and information on substratum consistency is limited. However, species richness hotspots along the SW Greenland shelf are concentrated at the shelf break, where bedrock predominates, facilitating the settlement of three-dimensional habitat-forming species like bryozoans, hydrozoans, sponges, and corals (Yesson et al., 2015; Gougeon et al., 2017). The southern Greenland Shelf, although narrow (50 km), offers a heterogeneous habitat with distinct geomorphology between the East and West coasts (Ryan, 2013). This diversity of habitat types likely contributes to the high taxon richness in the area (Zeppilli et al., 2016)

4.2. *Community differences between East and West Greenland*

The considerable differences in terms of hotspots of richness and biomass accumulations between West and East Greenland are likely driven by contrasting differences in oceanography, seabed geomorphology, such as moraines, troughs, canyons and banks and substratum availability between the two shelf areas (Roberts et al., 2021). The East Greenland Current (EGC) transports the majority of cold arctic water over the East Greenland Shelf towards southern Greenland and around Cape Farewell where it mixes with the warm Atlantic Irminger current and continues northwards along the West Greenland Shelf

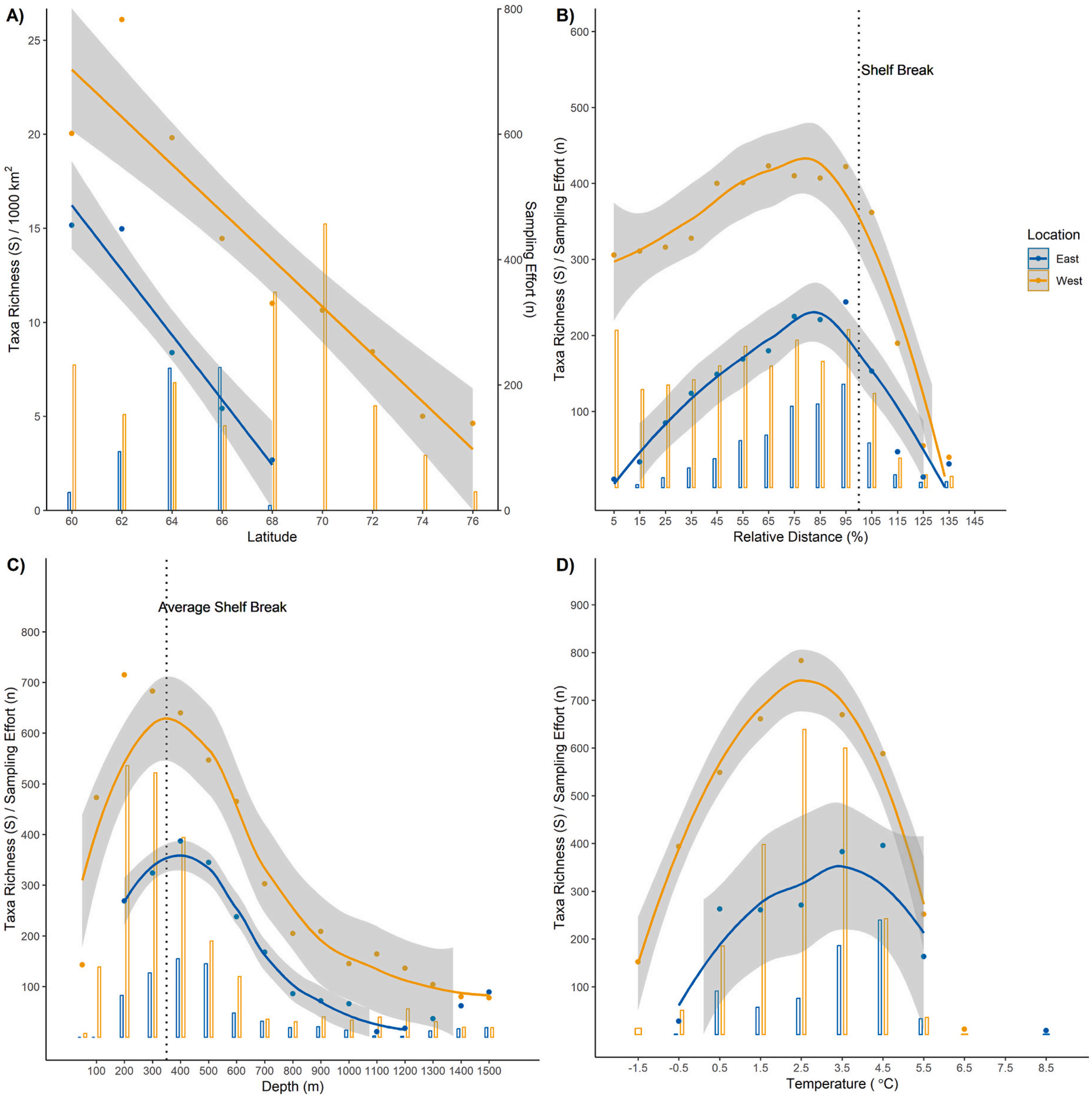

Fig. 6. Relationship of Taxon Richness for West (orange) and East (blue) Greenland across Latitude (A), with distance from shore (B), across Depth (C) and Temperature (D). Points represent total taxon richness and the line represents a fitted GAM (A) or LOESS (B–D) function with 95 % confidence intervals in grey. Bars represent total sampling effort within each category.

(Sutherland and Pickart, 2008; Qian et al., 2016). The large ostur (*Geodia* sp.) sponge communities found along the East Greenland shelf, which are primarily responsible for the striking discrepancy in biomass between the two coastlines seem to be a common and abundant feature in these parts of the North Atlantic that is influenced by the EGC and its descendants (Klitgaard and Tendal, 2004; Howell et al., 2016; Burgos et al., 2020). The most dominant ostur sponge species found within Greenland may be constrained to specific water masses in the North Atlantic (Roberts et al., 2021), explaining the lower abundance of some and disappearance of others along the West Greenland Shelf (Blicher and Arboe, 2021). This is also reflected in the lower observations of ostur sponges on the east coast of the Labrador Sea (Knudby et al., 2013). Interestingly, studies from NE Greenland (74–78°) have found low biomass and a minimum species richness of 297 taxa (Hansen et al., 2017). In West Greenland we only sampled to 77° yet observed a similar species richness of 234 taxa between 74 and 77°. This may indicate that the higher latitude regions could be more similar in terms of the biomass and richness they support, in both West and East Greenland. This may be driven by prolonged sea-ice cover, lower primary productivity and reduced availability of hard substratum in these regions (Witman et al., 2004; Rybakova et al., 2019).

4.3. *Greenland richness pattern in a global context*

Large-scale spatial patterns of species richness around Greenland generally align with established global trends, with some exceptions. We observed an expected decrease in species richness toward the North (Macpherson, 2002; Saeedi et al., 2019) and with depth (Costello and Chaudhary, 2017). Interestingly, Wei et al. (2020) noted an increase in richness toward the Arctic in the Canadian Arctic, with Baffin Bay exhibiting the highest diversity and lower diversity in the more southern Labrador Sea. Alfaro-Lucas et al. (2023) confirmed that the Canadian shelf of Baffin Bay has significantly greater species richness (61 taxa) compared to NW Greenland (16 taxa), although this discrepancy may be due to the previously lower sampling effort on the Greenlandic side as this study recorded 179 taxa between 75° and 77°N. In the East Atlantic,

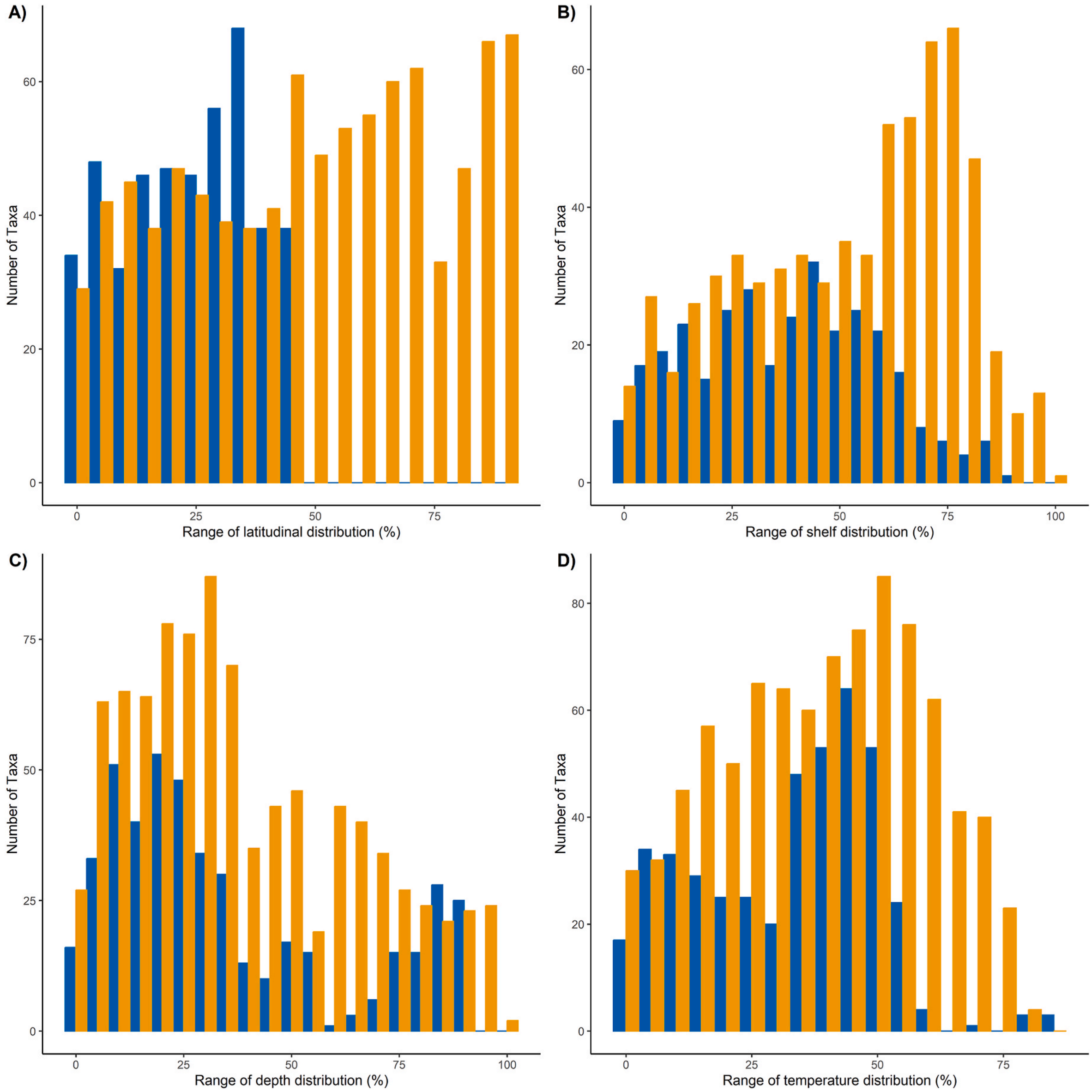

Fig. 7. Number of Taxa occupying different percentages of environmental ranges in West (orange) and East (Blue) Greenland for latitude (A), Distance from shore (B), Depth (C) and Temperature (D). Taxa only occurring once in the dataset have been excluded from this figure.

gamma diversity along the Norwegian shelf is primarily influenced by habitat heterogeneity rather than latitude (Ellingsen and Gray, 2002), also supporting Wei et al.'s (2020) assumption that habitat heterogeneity was driving richness in the Canadian Arctic. In Northwest Greenland, this suggests that species richness may not have been accurately captured, as also indicated by a low confidence index for this region. High-resolution studies of specific taxa can reveal more about richness patterns, when adjusted for sampling effort and depth of the seabed. Bryozoan richness, for example decreases with latitude in the North Atlantic, consistent with other taxa (Clarke and Lidgard, 2000). However, Denisenko & Blicher (2021) found that bryozoan richness increases again beyond 75°N, indicating a rise in endemic Arctic species compared to boreo-Arctic species at lower latitudes. This suggests that, similar to the Southern Ocean, the Arctic Ocean may harbour greater species richness than previously expected (Witman et al., 2004).

Consideration of richness and diversity change with depth has been an important topic in benthic ecology for a century, but no pattern was found by Gray (1994) off the Norwegian coast up to 300 m. Within that same depth range we found a taxon richness increase but then a subsequent decrease with depth down the continental slope and deep throughs. In the Southern Ocean, Brandt et al. (2007) found that faunal richness change from shelf to abyssal depths varied with taxon (meiofauna, polychaetes and bryozoans decreased but others increased or did not change). In Greenland richness was lower than expected in the shallows <100 m (Saeedi et al., 2019), yet showed a similar overall pattern compared with the wider Arctic (Saeedi et al., 2019). Complexities of richness with depth, such as shelf break peaks may be due to a confounding factor of exposure age. Barnes et al. (2016) found richness peaked at shelf locations beyond where ice was grounded at the last glacial maximum, which at South Georgia was often the shelf break. The Greenland icesheet also used to occupy large regions of the shelf which may have been responsible for the greater richness observed close to the shelf break (Simpson et al., 2009; Batchelor et al., 2024).

The observed decrease of richness with increased temperature was unexpected, as it was assumed that higher temperatures would typically be coincident with increased species richness (Tittensor et al., 2010). Yet, a similar trend was found for the Pacific Arctic (50° - 75°N), where the majority of epibenthic taxa (~78 %) showed a preferred temperature range between −1.4 °C and 5.1 °C (Logerwell et al., 2022). Similar to this study, only few species were found which persisted in temperatures up to 9 °C and again similar to this study, these were also the species with fairly large temperature ranges (Logerwell et al., 2022). This shows that, although Greenland hosts many boreal species found across the Atlantic, they clearly have adapted to the prevalent temperature regime here. A thinning of cold water layers and atlantification of these seas could thus lead to the loss of intraspecific diversity across the Atlantic (Pauls et al., 2013; Csapó et al., 2021).

4.4. Potential impact of mechanical disturbance on taxon richness

Mechanical disturbance such as demersal fishing or iceberg scour has been shown to have an adverse effect on benthic species richness and biomass (Hiddink et al., 2017; Zwerschke et al., 2021). In Greenland, the fishing pressure is comparatively low and focuses on discreet areas along the shelf edge and geomorphological features such as banks and troughs. Within areas with fishing pressure, richness and biomass have previously been found to be adversely affected (Long et al., 2021; Maier et al., 2024). This was also observed in this study, where lower biomass and richness were usually found in grid cells that included fishing pressure. Thus, the observed lack of species richness peaks close to the shore and towards shallower depths might be an artefact caused by low sampling effort (e.g. difficulty of sampling steep topography), iceberg scouring or demersal fishing. This study was primarily limited to the extent of the fisheries stock assessment, it is therefore likely that the few included coastal or shallow areas have been more heavily impacted by fishing with the expected knock-on effect to benthic communities there (Long et al., 2021). One such area is Disko Bay, which is a coastal area that has been subjected to intensive bottom trawling as well as intense iceberg scouring over the last few decades (Krawczyk et al., 2022). Although relatively well sampled, it seems characterised by (unsurprising) low species richness and biomass. Iceberg scouring is a strong structuring force for benthic communities in the deep Southern Ocean yet less so, in the Arctic owing to the smaller size of icebergs found here (Gutt, 2001). However, icebergs impacting shallow coastal habitats (50–100 m) which are common in the Arctic can decimate affected communities and interrupt ecosystem functioning, as has also been shown in the Antarctic (Zwerschke et al., 2021). In relatively pristine NE Greenland similar taxon richness for epibenthic megafauna between fjord and shelf regions was found. The greatest taxa richness was observed on a shallow bank in the middle of the shelf (Fredriksen et al., 2020) supporting the possibility that the low taxa richness observed in this work might be caused by sampling bias or mechanical impact.

4.5. Generalist nature of Greenland offshore benthos

One of the most interesting finds is that taxa in the study areas appear to be much more generalist, with broader environmental niches, than expected for a polar region. Over 20 % of the observed taxa cover at least 40 % of the total environmental gradient, with approximately 2 % and 1 % (excluding rare taxa) of species showing a range of over 70 % and only 10 % respectively. This could explain the distinct lack of geographic clustering into specific community types also observed by other studies in West Greenland (Maier et al., 2024), which were dominated by arctic-boreal species (Denisenko and Blicher, 2021). Atlantic arctic-boreal taxa typically have wide distribution ranges up to the Beaufort Sea (Ravelo et al., 2020). The reasons for this are manifold, but are likely related to the evolutionary age of the Arctic and the lack of isolation between the Arctic Ocean and the Pacific and Atlantic Ocean. The Arctic shelf is evolutionary much younger than the Antarctic. Whereas the Southern Ocean Circumpolar current isolated the Antarctic 30 million years ago, the Arctic, in its current climatic condition, has only formed approximately 2 million years ago (Rintoul et al., 2001; Flesche Kleiven et al., 2002), minimising time for species to evolve. The Arctic Ocean is, in contrast to the Southern Ocean, also well connected to both the Pacific and Atlantic through a number of out- and inflow shelves, including the exchange of deep water masses through the Fram Strait (Rudels and Carmack, 2022). A free propagule exchange between these regions may have curbed the evolution of distinct and endemic Arctic taxa, as has happened in the Antarctic (Dunton, 1992; Hardy et al., 2011). Studies carried out on specific phyla within the Arctic Ocean showed that only up to 4 % of the observed mollusc species for example are truly endemic, whilst the other 96 % are often also found in the Atlantic or Pacific (Krylova et al., 2013). As taxa were mostly identified based on their morphological traits, there could be the possibility that cryptic species were not recognized as a separate species which could contribute to the large ranges of some taxa in this study (Bluhm et al., 2011a; Hardy et al., 2011). This is an issue that is also common in the Southern Ocean (Sands et al., 2021).

5. Conclusion

Overall, it is now clear that the Greenland Shelf has, in an Arctic context, rich and diverse benthic communities. Although the current compendium of data supports the cline to more depauperate biota with increasing latitude the more important regional difference is between the East and West coast (as found in many taxa across continents, see Kaiser et al. (2020)). The richness, rarity, carbon held in biomass and high abundance of VME indicator taxa in both regions highlights the need for a comprehensive management plan. Although taxa distribution largely conformed to global and expected patterns at gross scale, the data highlights the relatively small, cold, thermal niche the majority of its taxa can be found in. In light of climate change, this raises concerns as an increase in water temperature could thus cause a loss of taxa across Greenland (Gjelstrup et al., 2022; Logerwell et al., 2022). Based on this initial baseline we could identify seven areas with high conservation index (Fig. 8a). We chose areas with a conservation index of 0.4 or greater. This represents areas with a mean richness, richness of rare and VME taxa in the 75th percentile of the sample distribution. This represented areas with a higher-than-expected richness (mean ± SD; 25.25 ± 20.24) with a mean of 115 ± 27 taxa, and 3 ± 1 rare and 10 ± 4 VME taxa (see also Table S1). The selected areas span a range of environmental conditions, such as latitude, depth, geomorphological complexity and based on the prevalent taxa – substratum type. They also cover large proportions of areas where a Greenland management approach is already in place (Fig. 8a) and largely correspond with priority areas recently identified for an Arctic management approach (James et al., 2024). Critically though, with the exception of the areas on the SW shelf, confidence in such appointed areas was low. Thus, we propose to direct immediate management effort towards those along the West coast and urgently focus further sampling campaigns towards the East and the North. Demersal fishing in discreet areas provides an important revenue to Greenland's society. Therefore, we suggest an adjustment of the conservation areas to avoid conflict between conservation goals and societal needs (Fig. 8b). This work provides a stepping stone towards understanding and protecting a notoriously understudied region, using a cost-effective sampling regime and could be adapted by other nations.

CRediT authorship contribution statement

Nadescha Zwerschke: Writing – original draft, Visualization, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Nanette Hammeken Arboe:** Writing – review & editing, Data curation. **Johanna Behrisch:** Writing – review & editing, Data curation. **Martin Blicher:** Writing – review & editing, Funding acquisition, Data curation. **David K.A. Barnes:** Writing – original draft, Conceptualization.

Data statement

Efforts are underway off establishing a Marine Spatial Planning

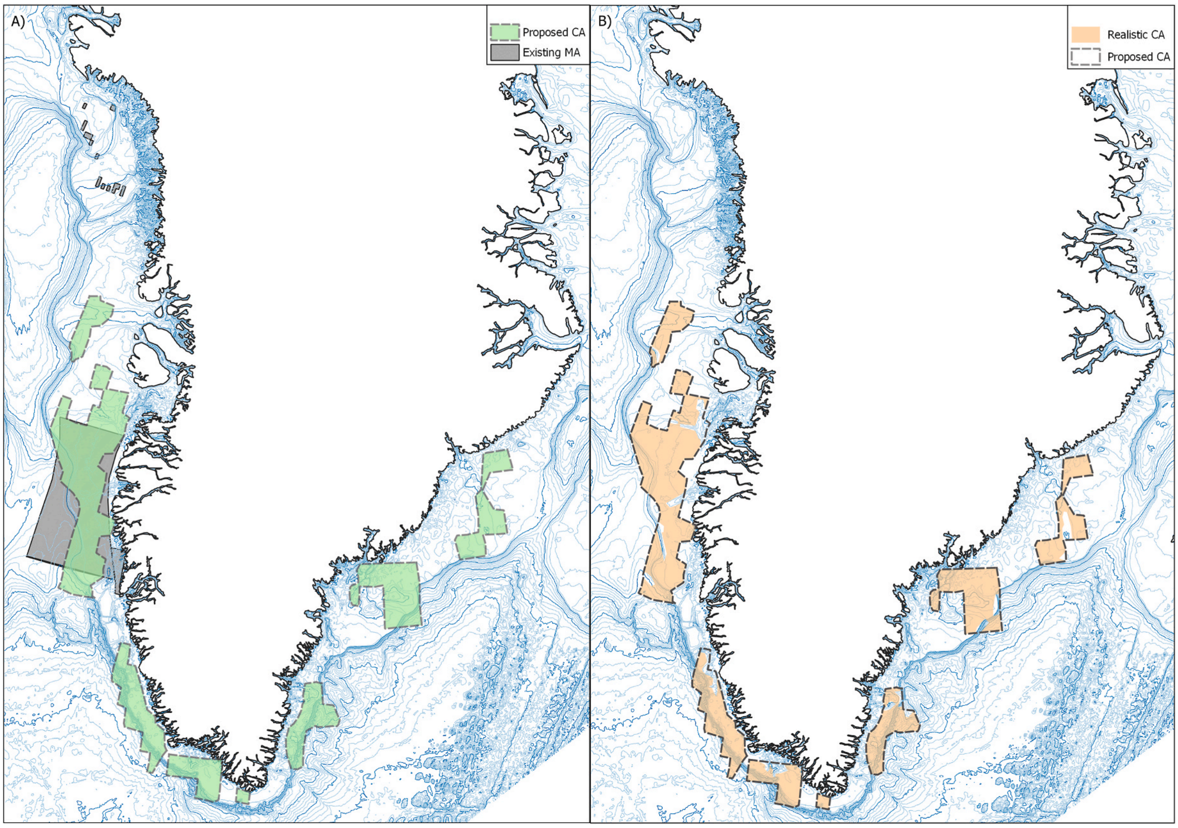

Fig. 8. Areas recommend for conservation efforts (CA) based on this study (area highlighted in green, A) and areas recommended for conservation avoiding potential conflict with demersal fishery hotspots (areas highlighted in orange, B). Already existing managed areas (MA) with no or limited bottom trawling are represented as grey checkered polygons. The large boundary box in the West limits trawling below 600 m.

platform in Greenland where data can be visualised online. Data used in this manuscript can be requested from GINR in the meantime, if the purpose of the proposed work falls within the Greenland research strategy and includes Greenland partners.

Declaration of competing interest

There is no conflict of interest between the authors.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.125285.

Data availability

Data will be made available on request.

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