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Arctic Benthic Seascapes

A trait-based perspective on benthic invertebrates around Greenland (Kalaallit Nunaat)

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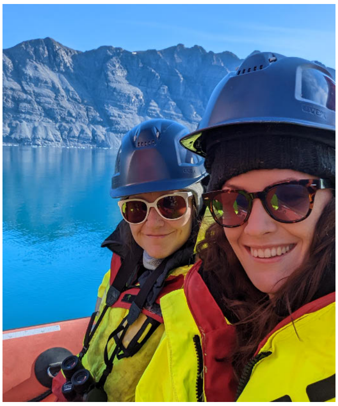

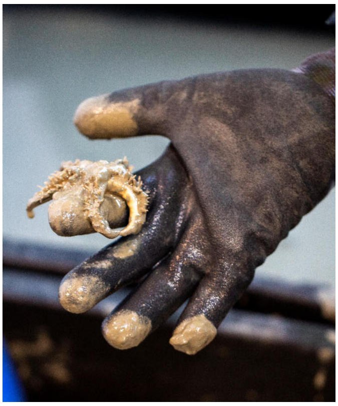

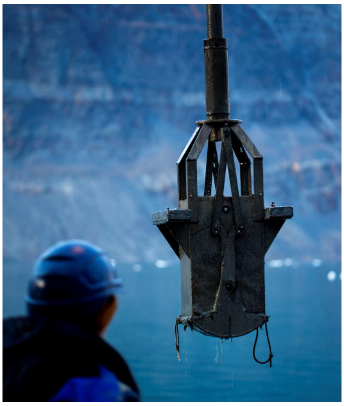

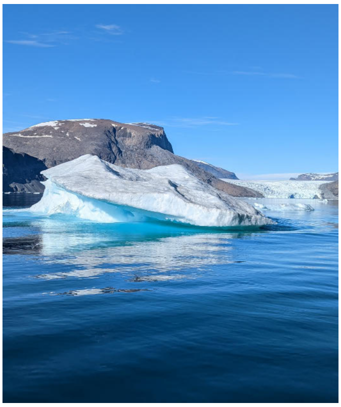

"Comfort is a drug.
Once you get used to it, it becomes addicting.
Give a weak person consistent stimulation,
tasty food, cheap entertainment
and they'll throw their ambitions right out the window.
The comfort zone is where dreams go to die."

Marcus Aurelius/Henry Cavill

Embarking on a scientific career is pushing yourself far beyond your comfort zone. As a scientist, you must know how to apply knowledge, challenge existing concepts, hypothesise ideas, collaborate, present, network, write concisely, be internationally savvy and highly organised in your time and thinking. Thus, being a scientist means keeping your mind open and never stopping learning; undertaking a PhD is training in being in the *un*-comfort zone, for which I am grateful to have the opportunity.

Abstract (in English)

The Arctic is warming substantially faster than the global average. This is resulting in declining sea ice, increased glacial melt and sedimentation, altered circulation patterns, and a changing water column structure, which is rapidly reshaping marine environments and biological communities. Understanding how benthic ecosystems are structured under these conditions is critical for predicting ecosystem trajectories.

Arctic benthic communities are species-rich and form a major component of marine biodiversity. They play a central role in carbon processing and storage, nutrient recycling, sediment modification, and energy transfer to higher trophic levels. These ecosystem roles are mediated by species' biological traits, capturing how organisms' function within their environment. Traits, such as feeding mode, mobility, dispersal and life-history strategies, represent ecological adaptations shaped by prevailing physical and environmental conditions. Consequently, understanding benthic responses to environmental change requires moving beyond species identity alone and considering the traits that determine how organism-environment interactions contribute to ecosystem processes.

Alongside advancing trait-based approaches, this thesis is motivated by multiple interacting pressures on Arctic benthic communities. First, fundamental knowledge of benthic trait composition remains limited across much of the Arctic, constraining our understanding of how environmental gradients structure ecosystem functioning at the seafloor. Second, northward species redistributions are increasingly documented; yet, benthic communities remain underrepresented in this context, despite their direct exposure to advected water masses and seafloor currents. If Boreal and Cosmopolitan taxa are increasingly present in Arctic benthic systems, this raises questions about functional compatibility, competitive interactions, and the long-term resilience of the ecosystem. Third, ongoing changes in freshwater input, stratification, and circulation are reshaping the delivery and redistribution of organic carbon at the seafloor, with implications for benthic biomass, food-web structure, and carbon storage. Through three complementary Papers **(I, II, III)**, this thesis applies a trait-based framework to address these knowledge gaps via integrating benthic community data, species traits, environmental gradients, and sediment-trap measurements across various habitats around Greenland.

A central synthesis emerging from this work is that the organisation of benthic communities around Greenland reflects environmental filtering acting primarily on species' traits rather than on species identity (taxonomy). Across regions and

habitats, pronounced variation in species composition was concurrent within a constrained trait space, such that communities converged on functional strategies suited to local hydrographic, sedimentary, and oxygen regimes **(I, II)**. This pattern indicates that substantial species turnover and biogeographic mixing can occur without a corresponding reorganisation of functional structure, provided that the environmental conditions defining the trait filter remain stable **(I, II)**. The strong explanatory power of traits for species responses to environmental gradients, coupled with the absence of similar responses among phylogenetically related taxa, further underscores that ecological vulnerability and resilience are shaped by functional characteristics rather than taxonomic relatedness **(I)**. Together, these findings emphasise that understanding Arctic benthic change requires a trait-based perspective, as environmental filtering constrains trait strategies and governs how communities reorganise under sustained environmental forcing.

This apparent functional stability further depends on benthic biomass being sustained by physical processes that deliver carbon and nutrients to the seafloor via both vertical and horizontal pathways in the water column. In Paper **III**, we identified a persistent three-layer water-column structure comprising surface, polar, and Atlantic waters across the three study systems in Northeast Greenland. With this hydrographic framework, benthic biomass and community composition were not consistently explained by vertical carbon flux alone. Instead, our results indicate that lateral transport and seafloor morphology shaped spatially heterogeneous carbon landscapes, with steep sills indicating down- and upwelling zones that support disproportionately high benthic biomass and functional diversity. As a result, benthic responses to ongoing climate change are likely to be expressed not only through shifts in species distributions but through changes in the spatial organisation of productivity, trait expression, and carbon utilisation across the Arctic seascape.

Overall, this thesis demonstrates that Arctic benthic ecosystem responses to climate change are influenced more by the constraining of trait space and the reshaping of carbon pathways at the seafloor than by species turnover alone. These findings establish a functional baseline against which future changes in productivity, trait selection, and carbon utilisation can be evaluated as Arctic marine systems continue to transform. By integrating trait-based ecology, this work provides a framework for interpreting benthic ecosystem reorganisation across Arctic seascapes, key for management and conservation.

Abstrakt/Sammanfattning (på svenska)

Arktis värms upp avsevärt snabbare än det globala genomsnittet. Detta leder till minskande havsis, ökad glaciärsmältning och sedimentation, förändrade cirkulationsmönster samt struktur av vattenkolumnen, vilket snabbt omformar marina miljöer och biologiska samhällen. För att kunna förutsäga utvecklingen i Arktis marina ekosystemen är det även avgörande att förstå hur botten(bentiska)ekosystem formas under dessa förhållanden.

Arktiska bottenfauna samhällen är artrika och utgör en central del av den marina biologiska mångfalden. De spelar en avgörande funktion i kolomsättning och kolinlagring, näringkretslopp, sedimentmodifiering samt energiöverföring till högre trofiska nivåer. Dessa ekosystemfunktioner upprätthålls av arters biologiska egenskaper. Egenskaper såsom födostrategi, rörlighet, spridningsförmåga och livshistoriska strategier representerar ekologiska anpassningar som formas av rådande fysiska och miljömässiga förhållanden. Följaktligen kräver en förståelse av miljöförändringars effekter att inte enbart artidentitet beaktas utan även de egenskaper som avgör hur interaktioner mellan organism och miljö bidrar till ekosystemprocesser.

Förutom att vidareutveckla egenskapsbaserade angreppssätt motiveras denna avhandling av flera kunskapsluckor gällande arktiska bentiska samhällen. För det första är grundläggande kunskap om sammansättningen av bentiska egenskaper fortfarande begränsad i stora delar av Arktis, inklusive nordöstra Grönland, vilket inskränker vår förståelse av hur miljögradienter strukturerar ekosystemfunktioner på havsbottnen. För det andra dokumenteras nordliga omfördelningar av arter i allt högre grad, men bentiska samhällen är fortfarande underrepresenterade i detta sammanhang, trots deras direkta exponering för olika vattenmassor och bottenströmmar. Om boreala och kosmopolitiska arter i ökande utsträckning etableras i arktiska bentiska system väcker detta frågor om funktionell kompatibilitet, konkurrensinteraktioner och ekosystemens långsiktiga motståndskraft. För det tredje omformar pågående förändringar i sötvatteninflöde, skiktning och cirkulation leveransen och omfördelningen av organiskt kol på havsbotten, med konsekvenser för biomassa, näringsvävsstruktur och kollagring. Genom tre kompletterande artiklar **(I, II, III)** tillämpar denna avhandling ett egenskapsbaserat ramverk för att tackla dessa kunskapsluckor genom att integrera bentiskt samhällsdata, arters egenskaper och miljögradienter i olika habitat runt Grönland.

Ett centralt resultat är att organisationen av bentiska samhällen runt Grönland återspeglar miljöfiltrering som i första hand verkar på arters egenskaper snarare än på deras taxonomiska tillhörighet. Över regioner och habitat förekom en uttalad variation i artsammansättning inom ett begränsat egenskapsutrymme, vilket innebar att samhällena blev mer lika i förhållande till funktionella strategier anpassade till lokala hydrografiska, sedimentära och syrerelaterade förhållanden **(I, II)**. Detta mönster tyder på att betydande artsomsättning och biogeografisk blandning kan ske utan motsvarande omorganisation av funktionell struktur, förutsatt att de miljöförhållanden som definierar egenskapsfiltret förblir relativt stabila **(I, II)**. Egenskapernas starka förklaringsvärde för arters respons på miljögradienter, i kombination med avsaknaden av liknande mönster bland fylogenetiskt närbesläktade taxa, understryker ytterligare att ekologisk sårbarhet och motståndskraft formas av funktionella egenskaper snarare än av taxonomisk släktskap **(I)**. Sammantaget betonar dessa resultat att förståelsen av förändring i Arktis bottenekosystem kräver ett egenskapsbaserat perspektiv, eftersom miljöfiltrering begränsar egenskapsstrategier och styr hur samhällen omorganiseras under långvarig miljöpåverkan.

Denna till synes funktionella stabilitet är dessutom beroende av att biomassan upprätthålls genom fysiska processer som levererar kol och näringsämnen till havsbotten via både vertikala och horisontella transportvägar. I artikel **III** identifierades en bestående treskiktad vattenpelarstruktur bestående av ytvatten, polart vatten och atlantvatten i de tre studiesystemen. Bottensamhällets biomassa och sammansättning kunde inte konsekvent förklaras av enbart vertikalt kolflöde, utan resultaten indikerar att lateral transport och havsbotten morfologi formade rumsligt heterogena kollandskap, där branta trösklar var kopplade till uppvällning och nedtransport och därmed stödde oproportionerligt hög bentisk biomassa och funktionell mångfald.

Sammantaget visar denna avhandling att responsen på klimatförändringar i arktiska bentiska ekosystem i högre grad påverkas av begränsningar i egenskapsutrymmet och omformningen av kolvägar på havsbotten än av artomsättning i sig. Dessa resultat etablerar en referenspunkt mot vilken framtida förändring i produktivitet, egenskapsselektion och kolutnyttjande kan utvärderas i takt med att arktiska marina system fortsätter att förändras. Genom att integrera egenskapsbaserad ekologi tillhandahåller detta arbete ett ramverk för att tolka omorganisationen av bentiska ekosystem i Arktis, vilket är av central betydelse för förvaltning och bevarande.

List of original publications

I. Armitage, P., Törnroos. A, Fredriksen, R., et al. 'Diverging Benthic Trait Diversity and Drivers across Fjord to Slope Habitats of the High Arctic'. *Estuarine, Coastal and Shelf Science* 313 (2025): 109086. https://doi.org/10.1016/j.ecss.2024.109086.

II. Armitage, P., Nordström, M.C., Oleszczuk, B., Legeżyńska, J., Włodarska-Kowalczuk, M., & Törnroos, A. (2026). 'Biogeographic diversity meets functional similarity: Trait convergence in benthic infauna from the Arctic ice-covered North to ice-free South'. *Diversity and Distributions*. https://doi.org/10.1111/ddi.70195

III. *As manuscript:* Armitage, P., Nordström, M.C., Svensen, C., Oleszczuk, B., Legeżyńska, J., Włodarska-Kowalczuk, M., & Törnroos, A. (2026). 'From Surface Flux to Seafloor Function: The Vertical Carbon Transport and Benthic Communities in High-Latitude Coastal Systems'.

Author contributions

CRediT (Contribution Roles Taxonomy)		I	II	III
Data	Data Collection	RF, BAB, EB, JSC, MCN	PA, AT	PA, AT, CS
	Data Curation	PA	PA, BO, JL, MWK	PA, CS, BO, JL, MWK
	Formal analysis	PA, BW	PA	PA
Study Design and Methods	Conceptualisation	PA, AT, MCN	PA, AT, MCN	PA, AT, MCN
	Methodology	PA, AT, BW, MCN	PA, AT, MCN	PA, AT, MCN
Manuscript prepartion	Visualization	PA, AT, MCN	PA	PA
	Writing – original draft	PA	PA	PA
	Writing – review & editing	PA, AT, RF, BAB, BW, EB, JSC, MCN	PA, MCN, BO, JL, MWK, AT	PA, MCN, CS, BO, JL, MWK, AT
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Armitage, P. (**PA**), Törnroos, A (**AT**), Nordström, M.C. (**MCN**), Fredriksen, R. (**RF**), Bluhm, B.A. (**BAB**), Weigel, B. (**BW**), Bonsdorff, E. (**EB**), Christiansen, J.S. (**JSC**), Svensen, C. (**CS**), Oleszczuk, B. (**BO**), Legeżyńska, J. (**JL**), Włodarska-Kowalczuk, M. (**MWK**).

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1. INTRODUCTION

At the time of writing this thesis, the Arctic is at the forefront of climate change studies. Over the past sixty years, global temperatures have been increasing, affecting ecosystems worldwide. Scientific evidence unequivocally attributes the pace of these changes to anthropogenic (human) activities (Rantanen et al., 2022; IPCC, 2023). The Arctic environment, which is the most sensitive to climate warming (Casagrande et al., 2021; IPCC, 2023), has dramatically shifted from an environment dominated by sea ice and glaciers to potentially being ice-free in the summers as early as the 2030s-2050s for the first time in ten thousand years (Wang and Overland, 2009; Rantanen et al., 2022; Kim et al., 2023; Rieke et al., 2023). The consequence of this change is causing interrelated shifts, which redefine not only the Arctic's physical landscape but also trigger complex ecological cascades that impact terrestrial, marine, and climate systems (Armstrong McKay et al., 2022; Kuletz et al., 2024).

While many Arctic fauna and flora are vulnerable to ongoing environmental changes, the often less familiar organisms living in and on the seafloor, collectively known as benthos (Box 1), are frequently overlooked. Yet, these species living at the seafloor form dense, diverse communities and play a fundamental role in marine ecosystems globally by providing a wide range of essential ecological functions (Grebmeier et al., 2015; Solan et al., 2020a). Specifically, Arctic benthic invertebrates are a key food resource to commercially important demersal fish (Greenlandic Cod, Halibut, Char, and Red Fish) and to even higher trophic levels, such as walrus, seals and sharks (Christiansen et al., 2016; CAFF, 2017; Grebmeier et al., 2018; Amiraux et al., 2023). They also recycle and remineralise nutrients, store and sequester carbon, and remove pollutants from the water column (Clarke, 1983; Solan et al., 2008). Yet these taxa are also vulnerable to the environmental changes in the Arctic and are disproportionately understudied compared to marine mammal, fish, and plankton ecology and distributions, leaving many knowledge gaps in our understanding of their role in the ecosystem and how it functions collectively.

This thesis examines the ecological understanding of zoobenthic communities in the Arctic environment, particularly through their biological traits. By investigating the direct and indirect relationships between climate change (rising temperatures, melting ice, altered habitats, and shifting species), benthic communities (species and traits), and ecosystem dynamics (interplay of benthos with bathymetry, currents and water masses), this research contributes to our understanding of benthic diversity, functional roles, and environmental dependencies across key Arctic regions through three complementary studies.

Box 1. Arctic benthic invertebrates represent some of the most phylogenetically and functionally diverse communities in marine ecosystems (CAFF, 2017). They comprise thousands of species inhabiting both within sediments as infauna and on the seafloor surface as epifauna, and are dominated by polychaete worms, crustaceans, bivalve molluscs, and echinoderms. Representative taxa include tube-building and sediment-reworking polychaetes such as *Spiochaetopterus* and *Maldane*, crustaceans ranging from amphipods to the commercially important northern shrimp *Pandalus borealis*, bivalves including thyasirids and nuculanids associated with microbially active sediments, and echinoderms such as brittle stars and sea urchins (Fredriksen et al., 2020; Kokarev et al., 2024; Maier et al., 2024; Piepenburg et al., 1996, 2011; Wlodarska-Kowalczuk et al., 2004). This diversity encompasses a vast range of variation in morphology, body size, life-history strategies, feeding modes, mobility, and reproductive traits, which collectively shape how benthic taxa interact with their environment (Clarke et al., 1983; Komendić et al., 2024; Wlodarska-Kowalczuk et al., 2012). Through suspension feeding, deposit feeding, predation, and active sediment reworking, these organisms regulate carbon processing by influencing organic matter burial and remineralisation, and mediate nutrient recycling across Arctic shelf and fjord systems.

Photo © the Nansen Legacy, (2024), adapted by the author.

1.1 Defining the Arctic environment

Using the latitudinal definition[1] (*i.e.,* the Arctic Circle at 66°34′ N), the Arctic is distinguished by extreme seasonal variation in sunlight, with increasing periods of continuous daylight in summer and darkness in winter as latitude increases (Berge et al., 2020). At the North Pole, this results in up to 177 consecutive days of complete darkness. Reduced solar input and prolonged darkness during winter allow air temperatures to drop to as low as −68 °C, while summer temperatures can reach approximately 10 °C, coinciding with extensive sea ice melt (Berge et al., 2020). Seasonal sea ice formation and melt play a crucial role in regulating Arctic climate and contribute to global ocean circulation through their impact on water mass formation and the large-scale ocean conveyor belt.

Beneath the ice and water column, the Arctic seafloor is highly dynamic and spatially complex (Arndt et al., 2015; Gougeon et al., 2017). Iceberg scouring, sediment redistribution, and glacial processes continuously reshape benthic habitats, while in some regions, human activities such as dredging, resource extraction, and seabed exploitation add further disturbance (Gutt et al., 1996; Jørgensen et al., 2019; Morrison et al., 2020). Arctic bathymetry spans deep ocean basins, yet the coastal regions (*e.g.,* Greenland, Svalbard (Norway), Canada, Alaska (USA), and Russia) are dominated by deep fjords and broad continental shelves characterised by steep gradients, sills, and troughs, as well as complex current systems (Arndt et al., 2015; Rignot et al., 2016; Wood et al., 2021). These shelf and fjord environments host high levels of biological diversity and productivity, representing key transitional zones where organic matter is transformed, retained, or exported, ultimately influencing the fate of carbon within Arctic marine ecosystems (Węsławski et al., 2011; Solan et al., 2020a, 2020b; Sutton et al., 2020; Bridier et al., 2024).

1.2 A rapidly changing Arctic climate

Global atmospheric warming, driven by rising carbon dioxide levels since the Industrial Revolution, has resulted in the Arctic warming up to four times the global average (Fig. 1A; CAFF, 2017; IPCC, 2023; Rantanen et al., 2022). Rising air and ocean temperatures have led to a marked decline in sea ice, from a winter maximum of 14–16 million km^2 to a summer minimum of approximately 4

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[1] Alternative definitions of the Arctic include sea-ice extent, the treeline, permafrost distribution, and climatic thresholds such as the 10 °C July isotherm or snow cover. These definitions vary over time, whereas latitude provides a stable, time-invariant reference for consistent comparison.

million km^2 (Fig. 1B), corresponding to a loss of 12.6 % per decade relative to the 1981–2000 average (Fetterer et al., 2025; Bliss et al., 2026). Additionally, warming is not confined to the atmosphere and surface ocean but is increasingly transmitted through the water column via changes in circulation and water mass structure (Wood et al., 2021; Callard et al., 2025). In the European Arctic region, this has manifested as enhanced inflow and shoaling of warm, saline Atlantic Water, a process known as Atlantification, which has reduced the thickness of the overlying cold Polar Water layer and increased the transfer of oceanic heat to continental shelf and fjord systems (Carmack et al., 2016; Gjelstrup et al., 2022; Richards et al., 2022). During the work of this thesis, Atlantic Water has been found as far North as inside the Northeast Greenland fjords, which are now simultaneously receiving freshwater from the Greenland Ice Sheet and oceanic heat through Atlantic Water intrusions, further melting glaciers at their base in the seafloor as well as at the surface (Rignot et al., 2016; Hill et al., 2017; Gjelstrup et al., 2022). Together, these changes create alterations in water stratification and circulation, affecting nutrient supply, residence times, and energy transfer, with consequences that extend from pelagic production to benthic habitats and carbon processing across fjord and shelf ecosystems (Solan et al., 2020a; Bridier et al., 2021; Von Appen et al., 2021; Schulz et al., 2022; Zhulay et al., 2023).

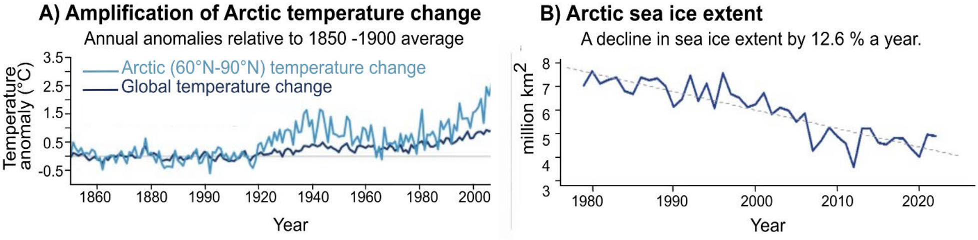


Figure 1. A) The difference between global and Arctic temperatures over 150 years. Data from Olsen et al., 2020. **B)** The Arctic sea ice extent during the September months since satellite observations started in 1979 (Fetterer (NASA), 2025).

The reduction of sea ice further amplifies warming through reduced surface reflectivity (albedo), and model projections suggest that the Arctic Ocean may become ice-free during summer as early as the 2030s–2050s, with the Barents Sea projected to lose year-round ice cover by the end of this century (Kim et al., 2023; Rieke et al., 2023). As the Arctic's climate undergoes rapid transformation, the region will experience some of the most pronounced physical, ecological, and socio-economic changes globally, given its high sensitivity to warming (Bae et al., 2021; Casagrande et al., 2021; Armstrong McKay et al., 2022; Bodur et al., 2024).

These changes are highlighted in Figure 2 and include, but are not limited to, accelerated glacial retreat, thawing permafrost, increased coastal erosion, altered precipitation patterns, and shifts in species distributions and shipping routes (Mouginot et al., 2019; Sejr et al., 2024). Together, these interrelated processes are reshaping the Arctic physical environment, the communities at the seafloor, and driving cascading effects, or ecological tipping points, across terrestrial, marine, and climate systems (Kortsch et al., 2012; Armstrong McKay et al., 2022; Kuletz et al., 2024).

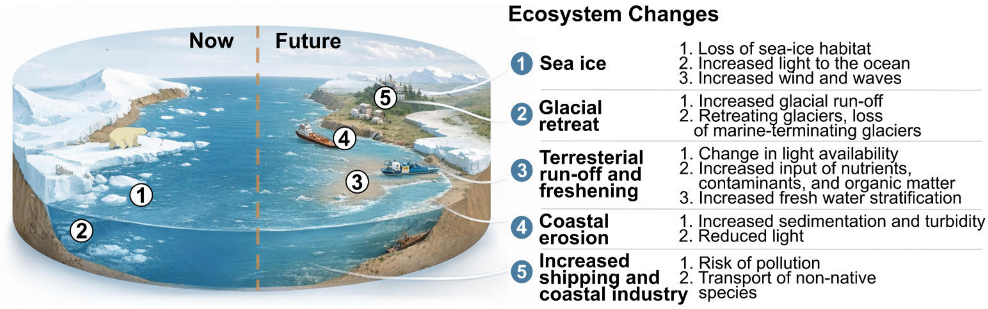


Figure 2. Schematic representation of current and projected Arctic environmental conditions. Circled numbers correspond to descriptions listed on the right. Adapted from Sjer et al. (2024) with graphical assistance from AI tools (ChatGPT Images, 2026).

1.3 How physical change translates to the seafloor

As glacial and sea ice melt, they create strong vertical stratification in the water column as well as deposit large amounts of glacial debris and sediments in coastal areas (Hill et al., 2017; Wood et al., 2021) Turbidity and water stratification, along with warmer Atlantic waters moving into the deep Arctic from the Eurasian Basin, are impacting the physicochemical structure in both the pelagic and benthic zones (Meire et al., 2017; Schulz et al., 2022; Bodur et al., 2024). Species are adapted to particular environmental conditions under which they perform optimally; when these physical regimes shift, communities may experience reduced resilience as environmental filters intensify, favouring taxa capable of tolerating the prevailing conditions (Barnes and Souster, 2011; Kortsch et al., 2012; Renaud et al., 2015; Al-Habahbeh et al., 2020; Pineda-Metz et al., 2020).

The Arctic continental shelves host some of the richest benthic communities worldwide, dominated by invertebrates such as echinoderms, bivalves, and arthropods (Piepenburg, 2005; CAFF, 2017; Oleszczuk et al., 2021). However, evidence from other polar regions demonstrates that physical changes at the seafloor often translate not only into changes in species composition or biomass, but also into fundamental shifts in functional roles and ecosystem processes (Al-Habahbeh et al., 2020; Solan et al., 2020b; Sutton et al., 2020). On the Antarctic continental shelf, ice retreat has been shown to reduce benthic abundance and biomass by up to two-thirds, with associated losses of key functional traits usually performed by benthic species (Barnes & Souster, 2011; Pineda-Metz et al., 2020). In the Arctic, long-term studies from Svalbard and the Barents Sea reveal that climate-driven species turnover is accompanied by changes in dominant trait strategies, including shifts in feeding mode, mobility, and habitat use, with cascading effects on food-web structure and species interactions (Kortsch et al., 2015; Yool et al., 2017). In some systems, environmentally driven changes in species composition have led to more profound ecosystem transitions, such as the replacement of hard-bottom benthic communities by macroalgal-dominated states (Kortsch et al., 2012; Al-Habahbeh et al., 2020). Such transitions reflect not only changes in species identity but also shifts in the functional characteristics of benthic communities that govern habitat structure, resource use, and ecosystem processes. Collectively, these examples highlight the importance of incorporating species' biological traits into benthic research (Box 2), as functional reorganisation can occur even when species richness remains relatively high (Frainer et al., 2021; Armitage et al., 2024).

Benthic invertebrates can be particularly vulnerable because many key traits constrain their ability to respond rapidly to altered environmental conditions. Limited adult mobility and restricted larval dispersal reduce the capacity of many benthic taxa to track shifting habitats, while long life spans, slow growth, and delayed reproduction are common among Arctic benthic species (Clarke, 1983; Włodarska-Kowalczuk et al., 2012; Meyer-Kaiser et al., 2022). These life-history traits reduce the capacity to avoid or rapidly respond to environmental change and slow rates of recovery following disturbance, particularly under changing circulation, sedimentation, and oxygen regimes (Morrison et al., 2020; Komendić et al., 2024). As a result, benthic communities may respond more slowly to environmental change than pelagic systems, but their trait composition can integrate and reflect long-term ecosystem reorganisation. This makes Arctic benthos especially valuable indicators of functional change at the seafloor, where shifts in traits translate into altered ecosystem functioning and services.

Box 2. Trait-based perspectives in benthic ecology

Trait-based ecology provides a mechanistic link between biodiversity, ecosystem functioning, and ecosystem services by focusing on what organisms do rather than on which species are present (Bremner et al., 2006; De Juan et al., 2022; Degen et al., 2018). This is particularly relevant for benthic research since benthic fauna regulate sediment oxygenation, nutrient cycling, and carbon transformation, via directly modifying their environment through bioturbation, bioirrigation, organic matter processing, and biogeochemical cycling, acting as ecosystem engineers at the seafloor (Meysman et al., 2006; Norkko et al., 2001; Snelgrove, 1997; Solan et al., 2020a). These processes support ecosystem functions and services, including habitat provision, food web stability, and carbon storage, ultimately contributing to human health and well-being (Costanza et al., 1997; Millennium Ecosystem Assessment, 2005). The common traits used in scientific research include behavioural (*e.g.,* mobility, feeding mode, sediment interactions), life history (*e.g.,* reproduction, larval development, and lifespan), and morphological characteristics (*e.g.,* size, shape, and fragility) (Bremner et al., 2006; Degen et al., 2018).

The environment does not affect all benthic species equally and can selectively filter organisms according to their traits (Pearson & Rosenberg, 1978; Sutton et al., 2021). Shifts in temperature, oxygen availability, sedimentation, or organic matter supply favour certain functional strategies while disadvantaging others, leading to changes in trait or functional composition (Al-Habahbeh et al., 2020; Kortsch et al., 2012; Pearson & Rosenberg, 1978; Sutton et al., 2020). Importantly, ecosystem functioning can change even when species richness remains relatively stable, making trait-based approaches particularly sensitive indicators of functional change compared to traditional taxonomic metrics (Frid & Caswell, 2015; Törnroos & Bonsdorff, 2012). By explicitly linking organisms to processes and services, trait-based benthic ecology provides a robust framework for understanding ecosystem resilience and vulnerability in a changing ocean (Bremer et al., 2006; Degen et al., 2018).

1.4 The potential ecological reorganisation of Arctic benthic communities

There is now substantial evidence that such biological reorganisation is already underway in the Arctic (see Kuletz et al., 2024, and references therein). Warming, changing circulation patterns, and increased light availability have been linked to northward range expansions and increasing dominance of boreal species across multiple trophic levels, from zooplankton (Richardson, 2008; Ratnarajah et al., 2023) to marine mammals (Heide-Jørgensen et al., 2023). Particularly around Svalbard and Greenland, changes in ocean circulation, along with boundary currents and shelf flows, can serve as transport pathways for pelagic life stages and mobile taxa, thereby increasing connectivity across previously distinct biogeographic regions (Csapó et al., 2021; Richards et al., 2022)(as an exemplar conceptual overview; see Fig. 3). This is reflected in northern fisheries. For example, Atlantic cod have expanded northward and increased in abundance around Svalbard, whereas cold-adapted, benthic-associated fisheries, such as northern shrimp (*Pandalus borealis*), have declined or shifted in distribution in parts of the Barents Sea and adjacent regions (Drinkwater, 2009; Wisz et al., 2015; Christiansen et al., 2016; Frainer et al., 2017; Andrews et al., 2019). Such patterns suggest a broader reorganisation of production pathways, potentially favouring pelagic-dominated systems (described in the next section, 1.5), but they also raise questions about how changing species assemblages may interact differently with the seafloor and overlaying water column. As described in section 1.3, shifts in species identity characteristically involve shifts in trait composition, and therefore in the functional roles that underpin benthic ecosystem structure.

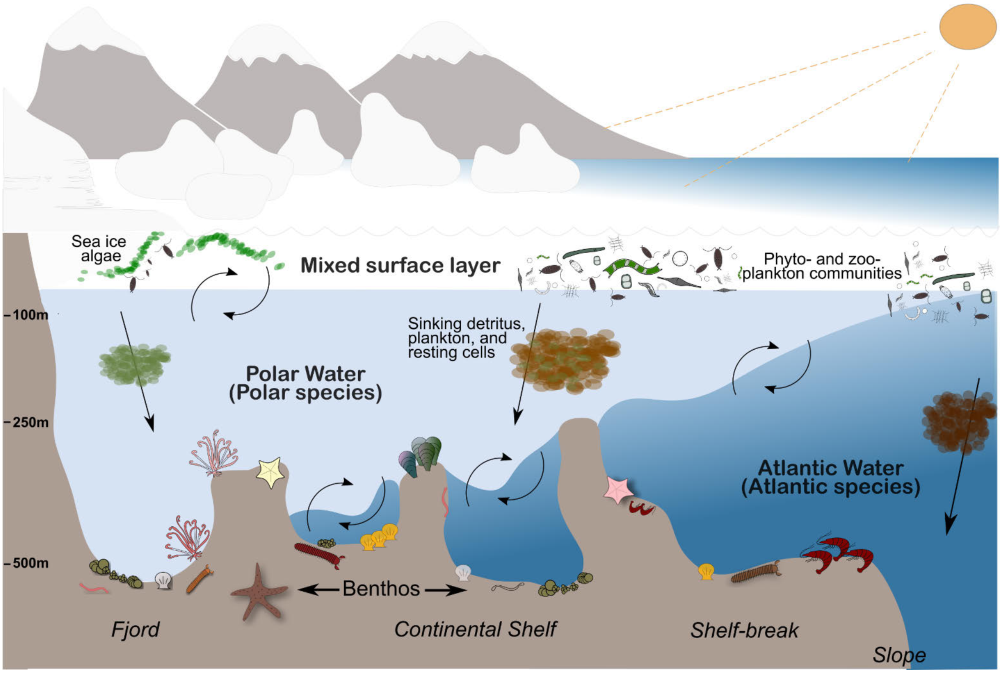


Figure 3. A schematic of the relationship between the expanding Atlantic water mass and its potential to impact polar environments through water stratification and the movement of species in the pelagic and benthic environments.

Species migrations, redistributions, or local extinctions effect changes in community assembly, including shifts in abundance, biomass, and species interactions. Importantly, the functional outcome of these changes depends on which traits are gained or lost as species redistribute, because trait turnover governs rates of bioturbation, suspension feeding, predation, nutrient regeneration, and ultimately the efficiency with which benthic systems store or remineralise organic carbon (Snelgrove, 1997; Solan et al., 2008; Pecl et al., 2017). Benthic species differ markedly in life-history and functional traits, with many Arctic taxa characterised by slow growth, limited dispersal, and specialised ecological roles, whereas cosmopolitan species often exhibit broader environmental tolerances, higher mobility, and greater reproductive capacity (Clarke, 1983; Grebmeier et al., 2015). As a result, biogeographic redistribution may represent not only a change in species' locations, but a reorganisation of the functional and competitive structure of benthic ecosystems.

Despite the growing body of evidence for species redistributions (Kuletz et al., 2024), Arctic benthic communities remain comparatively poorly understood, particularly infaunal assemblages, when contrasted with pelagic systems and higher vertebrates. While the arrival of some invasive or range-expanding species has been documented (Renaud et al., 2015; Goldsmit et al., 2020), far less is known about how Arctic benthic communities respond once new species begin to co-occur with native taxa. Questions remain as to whether these interactions result in displacement, altered competitive dynamics, functional redundancy, or, in some cases, enhanced resilience (Kortsch et al., 2012, 2015; Włodarska-Kowalczuk et al., 2012; Al-Habahbeh et al., 2020; Frainer et al., 2021). To structure and interpret such redistribution patterns, species are often grouped into broad biogeographic categories: Arctic taxa largely confined to high latitudes, Boreal taxa characteristic of sub-Arctic and temperate regions but capable of northward expansion, and Cosmopolitan taxa with extensive global distributions (Degen and Faulwetter, 2019). Understanding how widespread boreal and even cosmopolitan species integrate into, or disrupt, existing benthic communities is increasingly important, given the central role of benthos in nutrient cycling, carbon processing, and energy transfer to higher trophic levels (Degen et al., 2018; Wiedmann et al., 2020; Csapó et al., 2021).

1.5 Pelagic-benthic coupling and carbon transfer

The preceding sections emphasise the links between water column processes and benthic invertebrate communities. The interaction among these components, termed pelagic-benthic (or benthic-pelagic) coupling, describes the exchange of organic matter and nutrients between the pelagic realm and the seafloor, and is fundamental to the structure and functioning of Arctic marine ecosystems (Griffiths et al., 2017). Historically, this coupling has been strong due to the production of lipid-rich, fast-sinking organic matter from sea-ice algae and zooplankton, which efficiently transfers carbon and energy from surface waters to benthic communities (Clarke, 1983; Piepenburg et al., 1997; Bridier et al., 2021; Cautain et al., 2024). However, ongoing environmental change is altering this relationship.

Increased light availability following sea-ice retreat, freshwater input from melting ice, and the growing influence of Atlantic Water have enhanced surface primary production in some regions while simultaneously strengthening vertical stratification of the water column (Slagstad et al., 2015; Lewis et al., 2020; Schulz et al., 2022). This strengthened stratification can disrupt the downward transfer of nutrient- and organic matter-rich particles, shifting the balance between pelagic retention and benthic processing and reducing the delivery of organic carbon to the seafloor (Fig. 4) (Von Appen et al., 2021; Zhulay et al., 2023; Bodur et al., 2024). Furthermore, not only the magnitude of carbon export, but also its quality, degradation state, and mode of transfer to the seafloor can be impacted (Henson et al., 2019; Wiedmann et al., 2020; März et al., 2022).

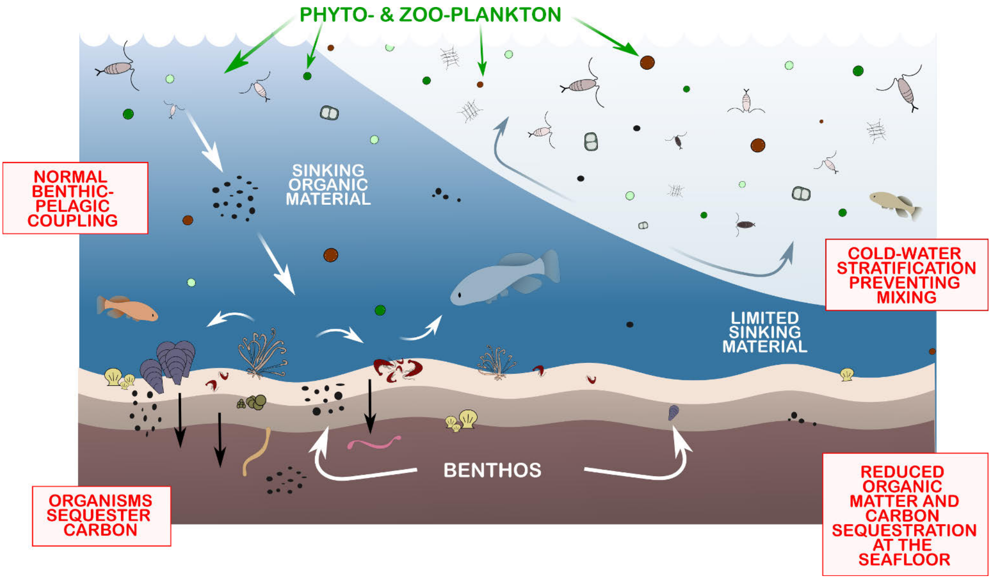


Figure 4. Schematic to visualise the disruption of water stratification in the polar regions impacts pelagic-benthic coupling and benthic invertebrate biomass.

Since Arctic benthic communities rely on pronounced seasonal pulses of organic matter, weakening of normal pelagic-benthic coupling affects benthic biomass, food-web structure, and higher trophic levels (Zhulay et al., 2023; Bodur et al., 2024; Cautain et al., 2024). Van Denderen et al. (2017) document a shift from coupled demersal–pelagic production pathways toward increasingly pelagic-dominated systems under strengthened stratification, driven by reduced food availability to benthic communities (Fig. 5). If sustained, these changes are expected to lower benthic invertebrate biomass, constrain demersal fisheries, and reduce carbon stored in benthic fauna, with broader ecological and economic implications for Arctic biodiversity, fisheries productivity, and carbon sequestration.

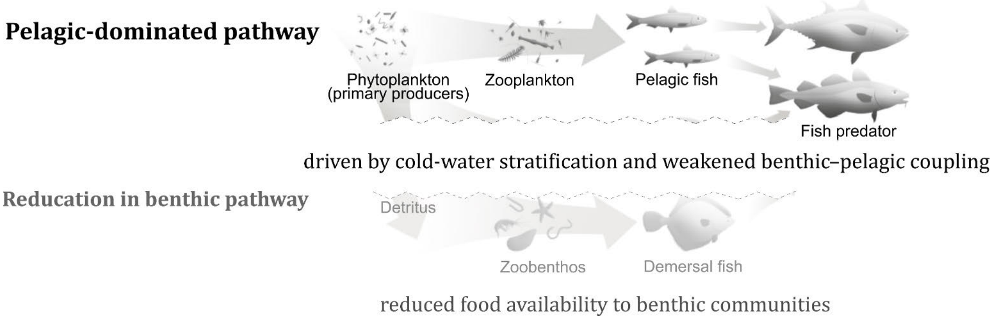


Figure 5. As climate changes, fish production is expected to shift to pelagic fish pathways, which are favoured in more stratified systems. Adapted from van Denderen et al., 2018.

While carbon research has become central to contemporary scientific and policy discourse, aimed at slowing the pace and impacts of climate change (CAFF, 2017; IPCC, 2023), most marine studies continue to frame carbon primarily as a vertical flux to the deep seafloor in open-ocean systems (Griffiths et al., 2017; Wiedmann et al., 2020; Visser, 2025). In contrast, coastal and shelf environments are responsible for disproportionately high carbon inputs, storage, and transformation, driven by terrestrial runoff, glacial discharge, shallow bathymetry, and strong biogeochemical coupling (Costanza et al., 1994; Luisetti et al., 2019). In Northeast Greenland, where circulation patterns, glacier dynamics, and complex fjord–shelf bathymetry interact, these processes are likely to exert a particularly strong influence on how carbon is delivered to, processed by, or bypasses benthic systems (Wiedmann et al., 2020; Bodur et al., 2024). Greenlandic fjord studies suggest that prolonged stratification and increased freshwater input can lead to more degraded and spatially heterogeneous organic matter reaching benthic habitats, with consequences for benthic energy uptake and storage (Bridier et al., 2019; Bao and Moffat, 2024). How carbon is utilised by benthic communities, and whether it is retained, transformed, or exported via benthic organisms under ongoing Arctic change, therefore represents a critical gap in linking physical forcing to benthic ecosystem functioning and carbon cycling.

2. THESIS AIMS

The overarching aim of this thesis is to advance understanding of how current Arctic benthic communities are structured in relation to taxonomic and trait distributions, and how these are organised within their present-day physical environment. Through three academic Papers (studies) that collectively span fjord, shelf, and slope systems around Greenland, this work integrates taxonomic distributions, trait-based ecology, biogeography, and pelagic-benthic coupling to examine community structure and ecosystem functioning across multiple Arctic regions and spatial scales.

Specifically, the thesis is structured around the following objectives:

1) **Characterise the functional structure and diversity of Arctic benthic communities** across large-scale Arctic habitats (fjord, shelf, shelf break and slope) and identify the environmental drivers that shape trait composition and community assembly at the seafloor.
2) **Classify and assess benthic community composition and traits in relation to species biogeography on the West Greenland shelf** with particular focus on the composition and coexistence of Polar, Boreal, and Cosmopolitan taxa and the implications for ecosystem functioning in a region influenced by surface sea ice and deep water Atlantification.
3) **Determine how benthic biomass and functional composition respond to sedimentary and water column carbon flux in different coastal systems** and identify the mechanistic links between hydrographic forcing, organic matter supply, and benthic carbon processing in Arctic fjord environments.

The first Paper **(I)** addresses the foundational question of how benthic functional diversity is organised across the Northeast Greenland continental shelf. Using a trait-based hierarchical modelling framework, it examines whether distinct habitats, ranging from fjords to slope environments, support functionally distinct benthic assemblages, and evaluates the extent to which environmental filtering, traits, and taxonomic relatedness shape benthic species distributions. This provides a baseline understanding of benthic functional structure in a region where such information has previously been sparse.

The second Paper **(II)** focuses on benthic infaunal communities along a latitudinal gradient on the West Greenland shelf, spanning the Arctic Circle. By explicitly incorporating species biogeographic affiliations and trait-based approaches, this Paper explores how benthic communities respond to gradients in ice cover, sediment characteristics, and water current properties. In doing so, it addresses emerging questions surrounding species distributions, trait convergence or divergence, and the potential consequences of increasing coexistence between Arctic, Boreal, and Cosmopolitan taxa at the seafloor.

The third Paper **(III)** shifts attention from community structure to ecosystem processes by examining how variability in carbon flux and water column structure influences benthic communities in Northeast Greenland fjords. By integrating sediment-trap measurements, hydrographic data, bathymetry, and benthic community surveys, this Paper aims to identify mechanistic links among hydrographic forcing, organic matter delivery, and benthic biomass and functional composition. This work directly addresses how carbon is delivered to, utilised by, and potentially retained within benthic systems under ongoing Arctic change amongst three unique high-latitude coastal systems.

Together, these three studies provide an integrated assessment of Arctic benthic communities across spatial scales and environmental gradients. By combining trait-based ecology, biogeography, and carbon flux dynamics, this work contributes to a more mechanistic understanding of benthic responses to climate forcing and offers a foundation for future studies seeking to link Arctic biodiversity change with ecosystem processes, environmental filtering and carbon cycling.

3. MATERIALS AND METHODS

3.1 Study regions and overall sampling design

This thesis synthesises three complementary studies that examine Arctic benthic community structure and function across the Greenland fjord and shelf environments. Together, the studies span West Greenland, covering a latitudinal shelf gradient across the Arctic Circle, and Northeast Greenland, including stations from fjords to slopes within the Northeast Greenland National Park (Fig. 6). Across these regions, benthic community sampling was integrated with environmental characterisation, trait-based analyses, and, in one study, direct measurements of particulate organic matter export through the water column. Across all Papers, the common goal is to link benthic biodiversity and functional composition to the surrounding environment.

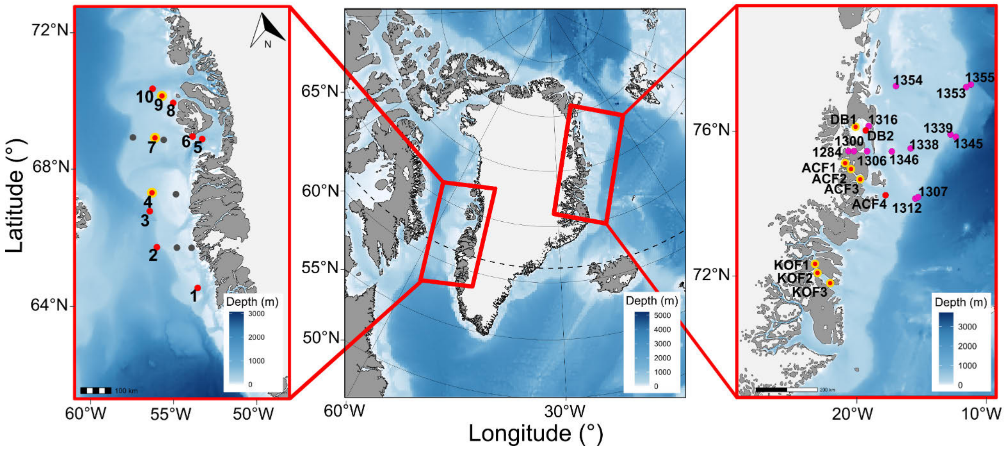


Figure 6. Map of the study sites along West (left) and Northeast (right) Greenland. Red stations are where box cores were taken, yellow ringed stations are where sediment traps were deployed, teal stations (right) are trawled stations, and grey stations are planned cruise stations, but no benthic sampling took place. Projection: polar stereographic; graticule spacing varies with projection.

3.1.1 The Northeast Greenland fjords, shelf and slope (I & III)

Papers **I** and **III** focus on Northeast Greenland and cover a latitudinal gradient from 72°N in the Kong Oscar Fjord complex to 80°N at the Belgica Bank area (Fig. 6, right). Situated in the Northeast Greenland National Park, the study region remains sparsely impacted by direct human pressures and therefore provides a rare pristine environment for studying climate-linked relationships with benthos (Aastrup and Boertmann, 2009; Christiansen, 2012; Fredriksen et al., 2020). Paper **I** covers the broader Northeast Greenland continental shelf, including fjords, shelf, shelf break, and upper slope habitats. Paper **III** focuses on three high-latitude coastal systems: Kong Oscar Fjord, Brede- and Ardencaple Fjord (treated as one fjord system), and Dove Bugt (an embayment with several nearby glaciers), which differ in sill bathymetry, glacier influence, and exposure to Atlantic Water.

Circulation along the Northeast Greenland margin is dominated by the southward-flowing East Greenland Current, which exports cold, low-salinity Polar Water from the Arctic Ocean, while Atlantic-derived waters can reach the shelf via recirculation pathways, including the Return Atlantic Current (Paquette et al., 1985; Schneider and Budéus, 1997; Arndt et al., 2015); see Fig. 7). In particular, transport of Atlantic Water across the continental shelf via the Return Atlantic Current has been linked to Atlantification of the Northeast Greenland shelf system (Gjelstrup et al., 2022). The interaction among Polar Water export, Atlantic Water intrusions, and freshwater inputs from glacial melt produces strong spatial contrasts in stratification, sedimentation, and organic matter delivery (Görlich et al., 1987; Arndt et al., 2015; Sejr et al., 2024), which are expected to structure benthic communities and benthic carbon pathways across Northeast Greenland fjords and adjacent shelf habitats (Holte and Gulliksen 1998; Włodarska-Kowalczuk et al. 2005, 2012).

3.1.2 West Greenland shelf system (II)

Paper **II** is based on the West Greenland shelf, spanning approximately 64°N in the Nuuk region to 71°N in the Disko Bay region (Fig. 6, left), and is sampled along a latitudinal gradient that encompasses strong contrasts in sea ice seasonality, hydrography, and sediment environments. The shelf is approximately 2,000 kilometres long and 40 to 250 kilometres wide, connecting to Baffin Bay, Davis Strait, and the Labrador Sea. The region contains banks and sills that enhance mixing and local productivity, and it receives freshwater and sediment inputs from multiple fjords and large outlet glaciers, including the Disko Bay system (Vernet et al., 2021; Schulz et al., 2022; Maier et al., 2024; Schmidt et al., 2025). This gradient provides a natural snapshot of contemporary benthic community organisation across conditions that are expected to shift under ongoing warming, Atlantification, and changing sea ice regimes.

Hydrographic conditions along the West Greenland shelf are structured by the interactions among several major current systems and water-mass sources

(Curry et al., 2011; Rysgaard et al., 2020). The West Greenland Coastal Current transports a mixture of relatively warm Atlantic-derived waters and colder Arctic waters along the inner shelf, while the West Greenland Current carries warmer and more saline Atlantic Water northward along the continental slope (Curry et al., 2011; Rysgaard et al., 2020; Schmidt et al., 2025). These currents interact with colder and fresher waters originating from Baffin Bay and the Canadian Arctic, creating a mosaic of overlapping water masses across the shelf. Recent observations indicate that the influence of Atlantic Water on the West Greenland shelf has become increasingly pronounced, consistent with ongoing Atlantification (Rysgaard et al., 2020; Mortensen et al., 2022; Schmidt et al., 2025). Together with complex seafloor topography and heterogeneous sediments, these interacting currents generate dynamic habitats that can structure benthic persistence and productivity across the shelf (Roy et al., 2014; Jørgensen et al., 2016; Yunda-Guarin et al., 2020; Maier et al., 2024). Such circulation may also facilitate the redistribution of taxa across biogeographic boundaries and contribute to the coexistence of species with contrasting life-history strategies (Gaylord and Gaines, 2000; Wisz et al., 2015; Csapó et al., 2021; Victorero et al., 2023; Maier et al., 2024).

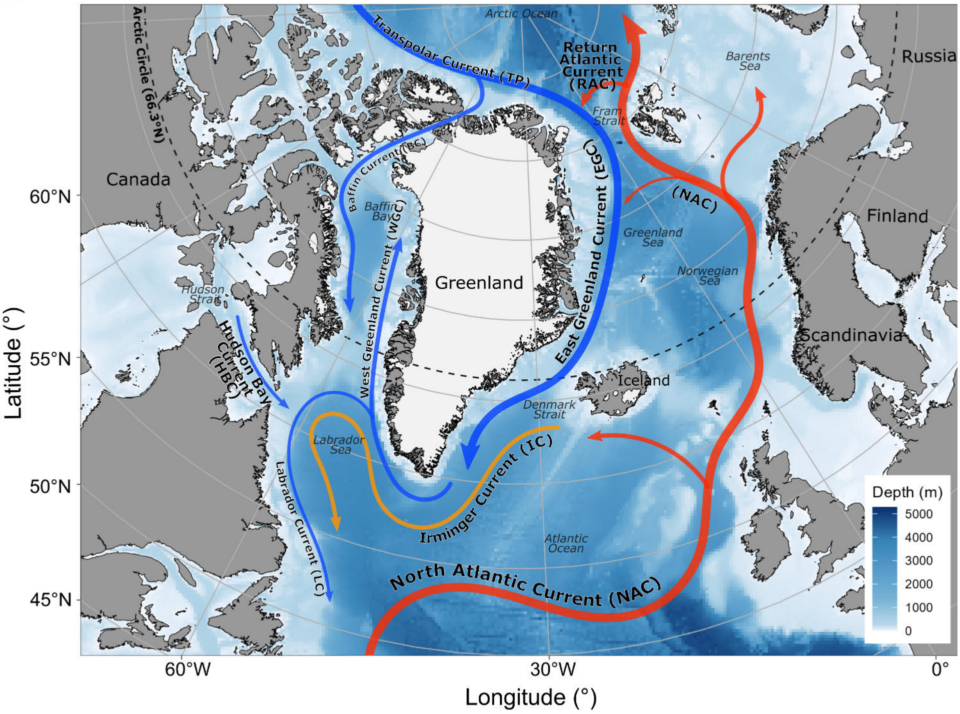


Figure 7. Major ocean current systems influencing Greenland and the wider Arctic Seas. Background shading shows bathymetry, with darker blues indicating greater depths. Warm Atlantic-derived currents are shown in red, including the North Atlantic

Current and its extensions into the Nordic Seas. Cold polar currents are shown in blue, including the East Greenland Current, West Greenland Current, and associated Arctic outflows.

3.2 Benthic sampling: cruise expeditions

3.2.1 Trawl sampling (I)

Epibenthic megafaunal invertebrates were collected through the TUNU Programme (UiT The Arctic University of Norway) in Northeast Greenland during research expeditions TUNU VI (2015) and TUNU VII (2017), using semi-quantitative Campelen 1800 shrimp trawls aboard RV Helmer Hanssen. Sampling covered 18 stations across fjord to slope habitats, spanning approximately 65 to 1,011 metres depth. The original species list was checked to the closest reliable taxonomic level and updated using WoRMS nomenclature, resulting in a final working set of 120 taxa for trait and community analyses. Abundance data were available for 2015 and 2017, and biomass data were available for 2017. Abundance and biomass were standardised to individuals and grams wet weight per 1 m^2.

3.1.2 Box core sampling (II, III)

Paper II: Infaunal macrofauna were collected along the West Greenland shelf during an ECOTIP research cruise in July 2021 aboard RV Dana. Benthic sampling was conducted at 10 stations, with ~3 quantitative box core replicates at each station and subsequent standardisation to individuals per square metre. One hard-bottom station (broken shell substrate), dominated by >1,000 small (<5 cm) brittle stars was excluded prior to analysis due to its huge difference in species and sediment composition, leaving a subset of stations designed to capture the main latitudinal and environmental gradients from box coring sampling.

Paper III: Infaunal macrofauna, hydrography, sediment characteristics, and short-term sediment trap fluxes were collected in August 2022 during the ECOTIP expedition aboard RV Maria S. Merian. Benthic sampling covered inner to outer fjord transects in each fjord system, with three box core replicates per station. Macrofaunal wet weight biomass was converted to carbon biomass using an established conversion factor, enabling a comparison between benthic biomass and carbon delivery metrics. Square root transformations were applied where appropriate to reduce heteroscedasticity and the influence of extreme values.

Papers II & III: Once infaunal macrofauna were sampled using a standard box corer, samples were sieved through a 1 mm mesh to retain macrofauna and then preserved in 70 % ethanol for later sorting and identification. Sorting and taxonomic identification were conducted in the laboratories of Åbo Akademi University and the Institute of Oceanology of Polish Academy of Sciences (IOPAN). Abundance or biomass was standardised to individuals or wet weight (g) per square metre. Where necessary, transformations were applied in subsequent analyses to mitigate the influence of highly abundant taxa and enhance the fit of statistical models.

3.3 Environmental measurements and sediment analyses

3.3.1 CTD-based water column variables

Across studies, near-bottom or bottom water properties (≤10 m from the seafloor) were obtained from CTD casts, including depth, temperature, salinity, oxygen, turbidity, and fluorescence. These were recorded using a Sea Bird SBE 911 system at each station and used as continuous predictors in statistical analyses. In Paper **I** the data was given processed, whereas in Papers **II & III**, CTD data were processed in Ocean Data View and combined with spatial descriptors and sea ice metrics. In Paper **III**, CTD profiles were also used to interpret water-mass structure and the presence of Atlantic Water in fjord systems via converting temperature to potential temperature (θ) to plot temperature-salinity diagrams.

3.3.2 Sea ice and water current variables

For Paper **II**, sea ice concentration data were obtained from Copernicus Marine Service products (European Union-Copernicus Marine Service, 2015) and summarised to represent the spatial gradient in seasonal ice conditions during the sampling year. Bottom current speed was extracted from Copernicus Ocean Physics products (European Union-Copernicus Marine Service, 2016) as monthly averaged velocity fields, selected to provide a proxy for circulation differences among stations when *in situ* current data were unavailable.

3.3.3 Sediment grain size and organic content

For Papers **II & III**, sediment subsamples were collected from each box core replicate for grain-size and organic content analyses. Organic content was quantified using Loss on Ignition (LOI), and carbon and nitrogen content were measured using mass spectrometry-based elemental analysis. Grain-size fractions were quantified using standard processing, including peroxide digestion of organic matter and SediGraph-based particle-size analysis, yielding the proportions of mud, silt, sand, and gravel. These sediment variables were used to represent substrate-based environmental filtering, depositional regime, and benthic habitat structure.

3.3.4 Seafloor bathymetry

For Paper **III**, multibeam bathymetric data were collected using a Kongsberg EM122 echosounder system aboard R/V *Maria S. Merian* during the ECOTIP expedition in August 2022. It was processed to describe coastal morphology, including sills, troughs, and depth structure along transects. Bathymetric profiles (depth, slope, aspect and ruggedness) were extracted along cruise transects using geographic information system software (QGIS, 2025) to contextualise sampling stations relative to seafloor morphology that may regulate Atlantic Water intrusion and sediment retention within inner coastal regions.

3.3.5 Sediment traps and particulate flux

Paper **III** uses data from short-term sediment-trap deployments with weighted mooring lines equipped with multiple cylindrical tubes at several depths per station. Trap samples were processed for phytoplankton composition, chlorophyll a, and particulate organic carbon and nitrogen following established protocols at The Arctic University of Norway (UiT, 2023). These measurements provided depth-resolved estimates of particle flux, enabling evaluation of how water-column structure, glacial proximity, and seafloor morphology influence the delivery of organic material to benthic habitats.

3.4 Trait compilation

Trait-based analyses were used across the thesis to interpret community distributions mechanistically. Traits representing behavioural, life history, and morphological characteristics were compiled primarily from the **Arctic Traits Database** (Degen et al., 2019; https://arctictraits.univie.ac.at), supplemented with targeted literature sources to preserve taxonomic resolution and minimise trait gaps. For Papers **I** & **II**, Traits were fuzzy-coded using a 0 to 3 affinity scoring approach to represent community-level flexibility across trait categories, whereas Paper **III** was converted to species-level information. A complete list of traits and the Papers in which they were included is provided in Table 1.

Table 1. Biological traits used across Papers I–III, with ecological interpretation and analytical rationale. Additional references are detailed in Paper I.

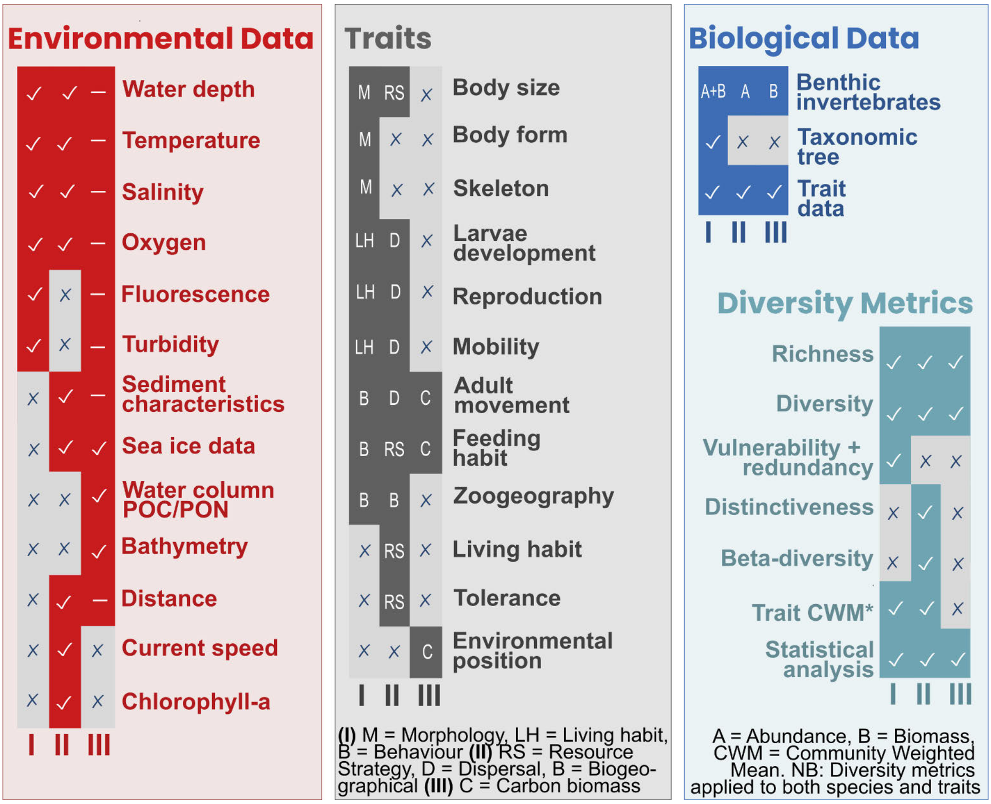
Trait	Trait Category	Rationale for inclusion	Paper(s) used
Adult Movement	MV1 Sessile/none MV2 Burrower MV3 Crawler MV4 Swimmer	A proxy for sediment–fauna relationships, trophic pathways, dispersal potential, and local carbon processing. Sessile taxa may dominate more food-rich fjord and shelf habitats, whereas mobile taxa may increase in patchy environments such as the shelf break and slope (Kristensen et al., 2012).	I, II, III
Body form	BF1 Globulose BF2 Vermiform BF3 Dorsoventrally compressed BF4 Laterally compressed BF5 Upright	Reflects adaptation to sediment type, burrowing ability, hydrodynamic exposure, and feeding mode. Body forms may vary across fjord, shelf, and slope habitats in relation to flow regime, substrate stability, habitat complexity, and sampling gear type. Included to link physical habitat structure and sediment dynamics to morphological adaptations. (Bremner et al., 2006b, 2006a).	I
Body size	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)	Proxy for life-history strategy, metabolic demand, growth rate, and vulnerability to disturbance. Body size may vary across fjord, shelf, shelf break, and slope habitats in relation to temperature, food availability, disturbance, and resource stability. Used to examine how environmental filtering and disturbance regimes structure functional capacity (Atkinson and Sibly, 1997; Dossena et al., 2012; Norkko et al., 2013; Mazurkiewicz et al., 2020).	I, II
Environmental position	EP1 Infauna EP2 Epibenthic EP3 Mixed	While influenced by sediment substrate and sampling approach, this trait provides insight into benthic–pelagic coupling, sediment carbon storage, and bioturbation. Increased sedimentation in inner fjord habitats may favour infaunal communities, whereas epifaunal taxa may be more present in exposed habitats e.g., shelf (Bolam and Eggleton, 2014; Costello et al., 2015).	III
Feeding habit	FH1 Deposit FH2 Filter/suspension FH3 Opportunist/scavenger FH4 Predator FH5 Parasitic	A core trait linking organisms to carbon pathways via biomass production, nutrient cycling, and trophic structure. Fjord habitats with high carbon export may favour deposit and suspension feeders, whereas more patchy food supply and greater hydrodynamic exposure across shelf-break and slope habitats may favour predators and opportunistic feeding strategies (Pearson and Rosenberg, 1978; Bremner et al., 2006b; Bolam and Eggleton, 2014).	I, II, III
Larval development	LD1 Pelagic/planktotrophic LD2 Pelagic/lecithotrophic LD3 Benthic/direct	Proxy for dispersal potential and connectivity. Cosmopolitan species are often associated with planktotrophic larvae that may track changing conditions more rapidly, whereas direct developers may be more locally constrained and are more common among Arctic species. Used to assess sensitivity and potential for recolonisation under environmental change (Thorson, 1950; Vance, 1973; Degen and Faulwetter, 2019).	I, II

Table 1. Continued.

Trait	Trait Category	Rationale for inclusion	Paper(s) used
Living habit	LH1 Free-living LH2 Crevice dwelling LH3 Tube dwelling LH4 Burrowing LH5 Epizoic LH6 Attached	Reflects the spatial coupling between organisms and their functional or behavioural relationships with the habitat or sediment, ranging from locally constrained to free-living strategies that exploit or modify sediments via bioturbation or bioirrigation (Degen and Faulwetter, 2019; Maier et al., 2024; Martins et al., 2025). This trait helped identify whether Arctic, Boreal and cosmopolitan species exhibited similar (competing) or distinct (complimentary) functional resource strategies across West Greenland.	II
Mobility	MO1 None MO2 Low MO3 Medium MO4 High	Strongly linked to feeding and movement strategies in terms of carbon processing and the ability to exploit resources. Increased mobility may enhance sediment reworking and bioturbation, whereas sessile taxa may dominate food-rich or advective habitats, such as the shelf. Central trait for ecosystem functioning, dispersal, and biological processes within and across sediments (Bremner et al., 2006b).	I, II, III
Reproduction	R1 Asexual R2 Sexual:external R3 Sexual:internal R4 Sexual:brooding	Reproductive strategy mediates community stability, reproductive investment, and mate availability across habitat gradients. Asexual reproduction may confer resilience in variable fjord environments, whereas brooding or external fertilisation may be more common across dynamic shelf and slope habitats (Thorson, 1950; Vance, 1973; Degen and Faulwetter, 2019).	I, II
Skeleton	SK1 Calcareous SK2 Siliceous SK3 Chitinous SK4 Cuticle SK5 None	Indicates trade-offs between protection, energetic cost, and sensitivity to disturbance or acidification. Skeleton type may vary across fjord and shelf habitats in relation to dominant taxa and sediment regimes (e.g. calcareous versus chitinous forms). Relevant for understanding vulnerability and carbon-related ecosystem roles under changing carbonate chemistry (Queirós et al., 2013; Beauchard et al., 2017)	I
Tolerance	T1 Low T2 Intermediate T3 High	Proxy for sensitivity to oxygen variability, sedimentation, and physical disturbance. Some Arctic species are known for being highly tolerant to sedimentation. Used to infer vulnerability and potential thresholds in environmental filtering (Degen and Faulwetter, 2019).	II
Zoography / biogeographic affinity	Z1 Arctic Z2 Arctic-boreal Z3 Boreal Z4 Cosmopolitan	Reflects historical exposure, physiological tolerance, and potential response to Atlantification (e.g., Arctic versus cosmopolitan species) and mixing. Used to interpret biogeographic mixing in relation to functional stability and trait convergence (Cardeccia et al., 2018; Degen and Faulwetter, 2019).	I, II

3.5 Statistical analyses and modelling strategy

Each Paper applied a different statistical strategy using combinations of environmental, biological, and trait data described in Sections 3.2 – 3.4. Primary datasets, including benthic species composition, environmental variables, and trait information, were used to derive secondary metrics such as species and functional diversity, community-weighted means, and measures of β-diversity. These derived indices were subsequently incorporated into multivariate and modelling approaches. The primary and secondary data used across Papers are summarised in Figure 8, and the analytical methods are outlined below.



Environmental Data

I	II	III	
✓	✓	–	Water depth
✓	✓	–	Temperature
✓	✓	–	Salinity
✓	✓	–	Oxygen
✓	×	–	Fluorescence
✓	×	–	Turbidity
×	✓	–	Sediment characteristics
×	✓	✓	Sea ice data
×	×	✓	Water column POC/PON
×	×	✓	Bathymetry
×	✓	–	Distance
×	✓	×	Current speed
×	✓	×	Chlorophyll-a

Traits

I	II	III	
M	RS	×	Body size
M	×	×	Body form
M	×	×	Skeleton
LH	D	×	Larvae development
LH	D	×	Reproduction
LH	D	×	Mobility
B	D	C	Adult movement
B	RS	C	Feeding habit
B	B	×	Zoogeography
×	RS	×	Living habit
×	RS	×	Tolerance
×	×	C	Environmental position

(I) M = Morphology, LH = Living habit, B = Behaviour **(II)** RS = Resource Strategy, D = Dispersal, B = Biogeographical **(III)** C = Carbon biomass

Biological Data

I	II	III	
A+B	A	B	Benthic invertebrates
✓	×	×	Taxonomic tree
✓	✓	✓	Trait data

Diversity Metrics

	I	II	III
Richness	✓	✓	✓
Diversity	✓	✓	✓
Vulnerability + redundancy	✓	×	×
Distinctiveness	×	✓	×
Beta-diversity	×	✓	×
Trait CWM*	✓	✓	×
Statistical analysis	✓	✓	✓

A = Abundance, B = Biomass, CWM = Community Weighted Mean. NB: Diversity metrics applied to both species and traits

Figure 8. Summary table of primary and secondary datasets used across the three Papers of this thesis. Columns I–III indicate the respective study Papers. A tick (✓) denotes variables included in the final analyses, an empty cell (×) indicates variables not used in that Paper, and a dash (–) denotes variables that were available but excluded from final models due to collinearity or covarying structure with other predictors.

3.5.1 Community structure and drivers (HMSC) (I)

For Paper **I**, epibenthic community structure was analysed using both abundance and biomass data. Trait composition was quantified using fuzzy-coded biological traits, and community weighted means (CWM) were calculated from trait-by-abundance and trait-by-biomass matrices (Laliberté et al., 2014). Taxonomic and functional dissimilarities among habitats were assessed using non-metric multidimensional scaling (nMDS; Kruskal, 1964), with Bray-Curtis dissimilarities applied to square-root-transformed taxonomic data (Bray and Curtis, 1957) and Gower distances applied to trait-based CWM data (Gower, 1971). Differences among habitats were tested using permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001). Biodiversity metrics included taxa richness and Simpson diversity, while functional metrics describing functional space and its occupancy included functional richness, functional divergence, vulnerability, and functional redundancy, calculated using distance-based trait approaches (Villéger et al., 2008; Mouillot et al., 2013). Differences among habitats were tested using analysis of variance (ANOVA) with Tukey post hoc comparisons, following assessment of variance homogeneity (Levene, 1960) and, where appropriate, the application of log or square-root transformations. Drivers of community composition were further examined using hierarchical modelling of species communities (HMSC), implemented as Bayesian joint species distribution models (Ovaskainen et al., 2017; Tikhonov et al., 2020). Models incorporated environmental covariates, species traits, and taxonomic relatedness, with model selection based on the widely applicable information criterion (WAIC; Watanabe, 2010). Variance partitioning was used to quantify the relative contributions of environmental, trait, and random effects, and model performance was evaluated using AUC and Tjur's R^2.

3.5.2 Biogeography, beta-diversity and the environment (MRM) (II)

Species were classified as Arctic, Boreal, or Cosmopolitan by integrating trait-based information from the Arctic Traits Database (https://arctictraits.univie.ac.at/) with global occurrence records from Global Biodiversity Information Facility (GBIF, https://www.gbif.org/), Ocean Biodiversity Information System (OBIS; https://obis.org/), and the World Register of Marine Species (WoRMS, https://www.marinespecies.org/) using latitude thresholds to define biogeographic affinity. A species was assigned to a category when more than 60 % of its records fell within the corresponding latitudinal range, with classifications cross-validated against existing trait definitions and expert knowledge. Taxonomic and functional diversity metrics were calculated at both α- and β-scales. Species and functional β-diversity were decomposed into turnover and nestedness components to distinguish species or trait replacement from richness-driven differences (Baselga, 2010, 2013). Functional β-diversity was quantified using trait-based dissimilarities to assess whether spatial change reflected functional turnover, functional convergence, or variation in trait richness (Villéger et al., 2008; Baselga, 2010; Cardoso et al., 2014). Collinearity among environmental variables was addressed by grouping predictors into water mass properties, sediment characteristics, and spatial–climatic structure, followed by principal component analysis (PCA) for each group to retain major composite gradients while preserving environmental information. PCA axes that explained ~98 % of the variance were retained and used in place of the original variables. To link ecological dissimilarity to environmental gradients, Multiple Regression on Distance Matrices (MRM) was applied, modelling pairwise taxonomic and trait dissimilarity as a function of multivariate environmental distance (Goslee, 2010; Legendre and De Cáceres, 2013). An automated model selection procedure evaluated all combinations of environmental PCA axes, selecting the best-performing models based on explained variance and permutation-based significance. Individual predictors from the optimal composite models were subsequently assessed to quantify their relative contributions to community composition and trait structure across biogeographic groups.

3.5.3 Linking carbon supply and benthic biomass (GLLVM) (III)

In Paper **III**, species wet weight biomass was converted to carbon equivalents using published conversion factors, allowing benthic biomass to be directly compared with measurements of organic carbon delivery and potential carbon retention. Traits were selected and analysed at the individual level to characterise benthic communities in terms of dominant functional strategies rather than taxonomic identity, allowing assessment of carbon pathways and ecosystem functioning at the level of functional groups (Degen et al., 2018; Degen and Faulwetter, 2019). Species-level carbon biomass was determined from fuzzy-coded traits describing feeding mode, mobility, and environmental position to construct trait–carbon biomass matrices and truncated to retain traits representing ≥ 95 % of total benthic carbon biomass in order to reduce noise from rare taxa. Environmental predictors were screened using summary statistics and correlation structure, and a reduced predictor set was selected to represent benthic carbon supply and depositional context. Based on collinearity assessment, only vertical particulate organic carbon flux and sediment carbon content were retained, while strongly correlated variables (including temperature and water column flux C:N) were excluded. All predictors were standardised prior to modelling.

Generalised linear latent variable models (GLLVMs) were fitted to trait-level carbon biomass matrices to examine relationships between carbon supply and benthic functional composition while accounting for residual covariation among sites (Niku et al., 2019). Models were fitted using a Tweedie distribution to accommodate continuous biomass data with zero inflation (Tweedie, 1986). A series of models with zero to three latent variables were evaluated, with model selection guided by the corrected Akaike Information Criterion (AIC). Fjord identity was evaluated as a random effect to account for shared structure within fjord systems. The selected model, containing a single latent variable, was used to quantify trait-specific responses to carbon flux and sedimentary carbon, while the latent axis captured residual structure attributable to unmeasured hydrodynamic or geomorphic processes.

3.6 Software environment and reproducibility

All statistical analyses were conducted in **R** (R Core Team, 2024), with packages selected according to the analytical requirements of each Paper. Functional diversity metrics and trait-based indices were calculated using the packages **FD** (Laliberté and Legendre, 2010; Laliberté et al., 2014), **BAT** (Cardoso et al., 2015), and **adiv** (Pavoine, 2020). Community composition analyses and multivariate ordinations were performed using **vegan** (Oksanen et al., 2022), while beta-diversity decomposition was performed using **betapart** (Baselga and Orme, 2012). Distance-based modelling and regression on distance matrices were conducted using **ecodist** (Goslee, 2010).

Joint species and trait–environment modelling was carried out using **HMSC** (Ovaskainen et al., 2017; Tikhonov et al., 2020) and **gllvm** (Niku et al., 2019) for the latent modelling approach. Data wrangling and visualisation were primarily performed using the **tidyverse** R packages, including **dplyr**, **tidyr**, and **ggplot2** (Wickham, 2016), with final graphics completed in **Inkscape** Software (Inkscape Project, 2020). Spatial data processing and mapping were conducted in **QGIS** (QGIS Development Team, 2024), while CTD data processing and visualisation were supported by **Ocean Data View** (Schlitzer, 2023) for Paper II and standardised processing routines for Paper III.

4. RESULTS AND DISCUSSION

The three papers of this thesis collectively provide a multi-scale assessment of Arctic benthic ecosystems across contrasting regions and environmental settings. Together, their findings offer an integrated understanding of community structure, trait composition, and environmental dynamics that extends beyond the individual studies. Section 4.1 first summarises the principal findings of each paper, and then Section 4.2 synthesises these findings to examine the processes structuring Arctic benthic communities across environmental gradients and spatial scales. This synthesis demonstrates how environmental filtering, trait-mediated responses, and physical seascape context jointly shape benthic community structure and ecological functioning.

4.1 Overview of results

Paper I: Diverging spatial patterns in functional diversity.

This study analysed epibenthic community composition across fjord, shelf, shelf-break, and slope habitats in Northeast Greenland to identify the dominant traits and drivers structuring Arctic benthic assemblages. Species richness and composition varied strongly across the region, with fjord and shelf habitats supporting more diverse communities than slope environments, resulting in pronounced differences in species composition across the seascape. Hierarchical multispecies modelling showed that depth, salinity, and oxygen availability explained a substantial proportion of variation in species distributions, whereas temperature contributed comparatively little explanatory power. Importantly, incorporating species traits significantly explained variation in species responses to environmental gradients, demonstrating that species–environment relationships were mediated by functional characteristics rather than taxonomy alone. Traits related to feeding mode, mobility and living habit helped explain why species occupied specific parts of the fjord–shelf–slope habitats. Overall, the results demonstrate that Northeast Greenland epibenthic communities are structured by environmental filtering, which acts through habitat-related water conditions, with species traits playing a key role in shaping community composition. The study highlights the importance of integrating environmental and trait-based approaches to understand how environmental gradients and functional traits interact to structure Arctic benthic ecosystems.

Paper II: Biogeographical overlap and functional convergence. This study analysed benthic community composition along the West Greenland shelf to assess how environmental structure and species biogeography interact and shape Arctic benthic assemblages. The shelf supported high species richness, with Arctic, Boreal, and Cosmopolitan taxa each contributing approximately one-third of the community. However, the assemblages varied strongly among stations, resulting in high β-diversity driven primarily by species turnover rather than nestedness. Despite these taxonomic differences, trait composition was remarkably consistent across the shelf, with the same dominant trait strategies expressed irrespective of species classification. Environmental analyses revealed that species composition was best explained by combinations of correlated variables, including sediment properties, water mass characteristics, and spatial structure, which were captured more effectively by a multivariate PCA framework than by single predictors. Together, these results suggest that West Greenland benthic communities are structured by strong environmental filtering that selects for a narrow set of viable functional traits, therefore occupying similar ecological roles, regardless of species identity or biogeographic classification.

Paper III. Beyond vertical flux: latent influences on benthic carbon. This study examined pelagic-benthic coupling across three Northeast Greenland coastal systems by integrating sediment-trap measurements, hydrographic profiling, sedimentary carbon analyses, and trait-based benthic community data. Although vertical particulate organic carbon (POC) export and sedimentary organic carbon (SOC) varied among systems and stations, they showed no consistent relationship with benthic carbon biomass. Stations with the highest POC or SOC did not necessarily support the greatest benthic biomass, while several sites with moderate or low carbon supply exhibited high biomass and functional diversity. Trait-based analyses indicated that only a subset of functional strategies, particularly suspension/filter-feeding taxa, showed consistent associations with carbon availability, whereas infaunal deposit feeders and burrowers showed weak or no responses to carbon metrics. Latent variable modelling identified an additional ecological gradient, independent of measured environmental predictors, that structured benthic biomass and was most consistent with steep and heterogeneous bathymetry. Overall, the results demonstrate temporal decoupling between vertical carbon export and benthic biomass, and indicate that hydrographic and seafloor conditions are significant for benthic responses and lateral carbon supply in Arctic coastal systems.

4.2 Synthesised understanding

4.2.1 Environmental filtering: beyond single predictors

A central synthesis emerging from this thesis is that Arctic benthic communities are structured primarily by environmental filtering operating through coupled physical and biogeochemical conditions, rather than by any single predictor acting in isolation. Across fjord, shelf, and slope habitats in Northeast Greenland (**I**) and along the West Greenland shelf (**II**), benthic assemblages were consistently explained by depth, salinity, oxygen availability, sediment properties, and spatial context, with temperature (a commonly used explanatory variable) contributing mainly as an indirect indicator of water mass structure, stratification, and circulation. Where temperature was included, it either explained less of the variation than co-occurring variables (**I**) or was strongly correlated with them (**II**, **III**). In each Paper, several covariates were found to be correlated (Fig. 9), underscoring that benthic communities around Greenland respond to integrated environmental regimes rather than single drivers. Multivariate analyses in the West Greenland study (**II**) further demonstrated that community composition responds to composite environmental gradients that capture the joint effects of hydrography and sedimentary structure, providing strong evidence that environmental filtering in deep Arctic benthic systems emerges from interacting and correlated drivers rather than simple one-to-one driver–response relationships.

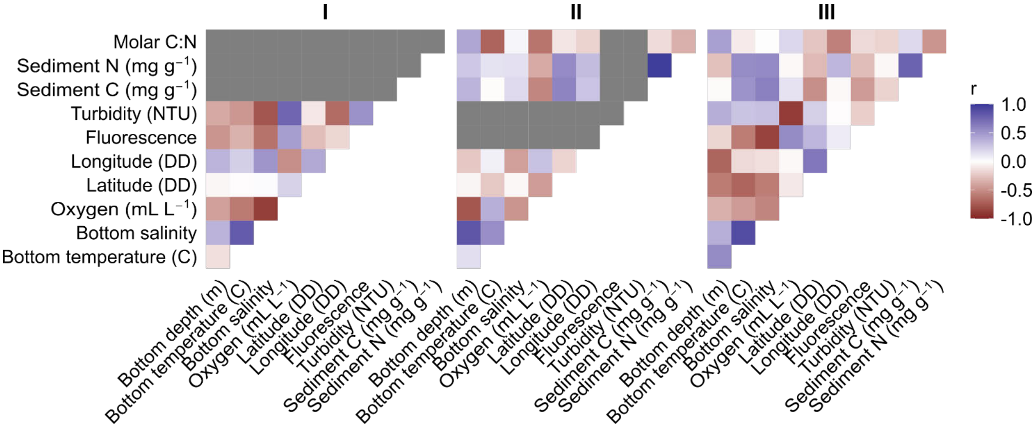


Figure 9. Pearson correlation matrices of environmental variables on the seafloor by Paper (**I-III).** Colours indicate correlation strength and direction (r), with red denoting negative and blue positive relationships. Grey cells indicate unavailable data.

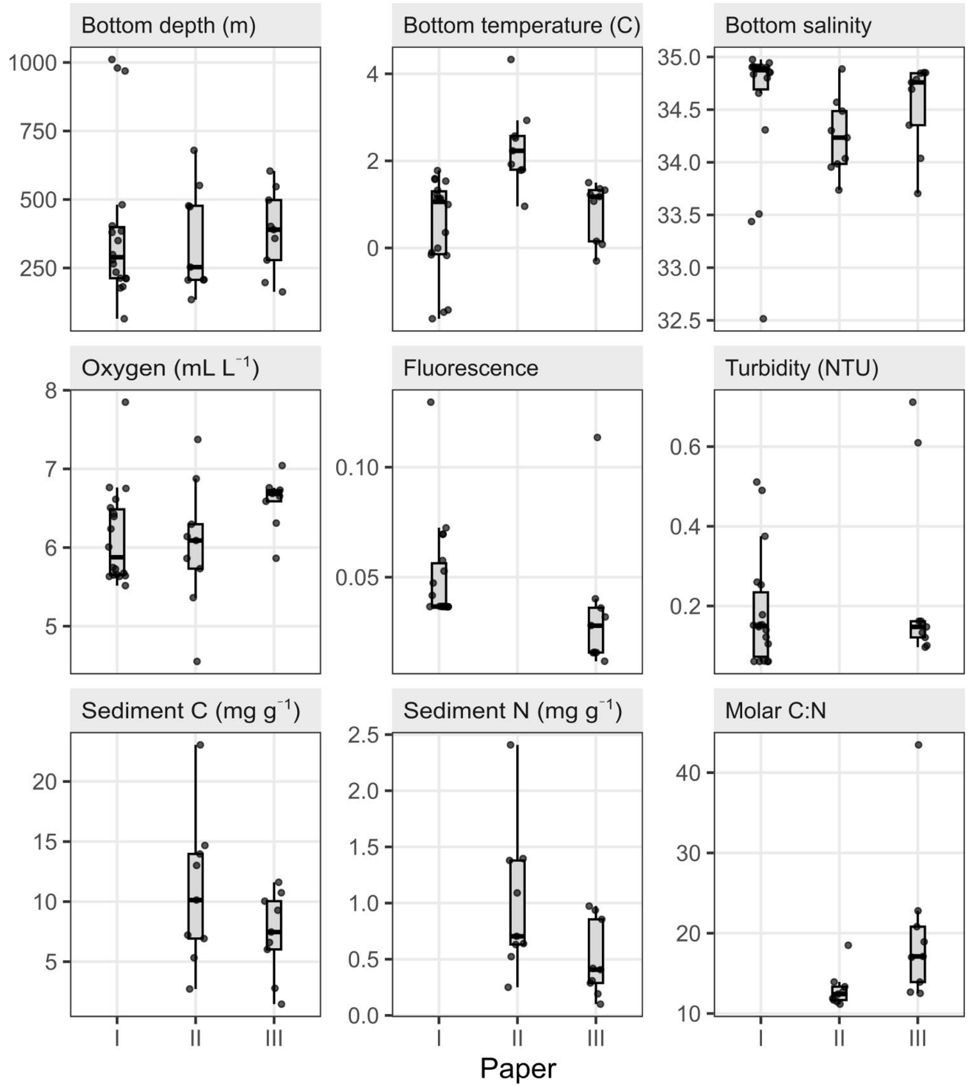


Figure 10. Distribution of bottom environmental conditions across the three Papers representing Northeast Greenland fjord, shelf and slope habitats (**I, III**) and the West Greenland shelf (**II**). Missing data are left blank. Boxplots show the median, interquartile range and full data spread, with points representing individual stations. Axes units correspond to those given in each panel heading.

An additional insight that relates to composite environmental gradients is the relatively constrained range of bottom conditions characterising both Northeast and West Greenland study systems. Despite differences in geography, sampling year, and habitat type, bottom temperatures generally ranged between approximately 0 and 2 °C, salinity between 33.5 and 35, oxygen concentrations between 5.5 and 6.5 µmol (Fig. 10), and sediments were consistently mud-dominated (>73 % mud). West Greenland stations were on average warmer (**II**) than those in Northeast Greenland (**I, II**), likely reflecting a warmer Atlantic Water influence (Curry et al., 2011), while lower oxygen concentrations were primarily associated with deeper shelf break and slope stations in Northeast Greenland (**I**). Salinity was lower in the shallow fjord environments of Paper **I**, but in the later Northeast Greenland study (**III**), deep fjord basins adjacent to glacial termini exhibited environmental characteristics more closely resembling shelf environments from Paper **I**. Notably, the strongest environmental contrasts were observed within the habitat classifications of Paper **I**, whereas Papers **II** and **III** largely sampled environments that fell within the same classifications defined by those earlier habitat types. This suggests that while environmental variables are correlated and structured across broader spatial regions (*e.g.,* fjord, shelf, slope habitats), they also operate within relatively narrow and persistent ranges typical of Arctic bottom waters (Clarke, 1983; Renaud et al., 2019). Environmental filtering in these deep systems therefore appears to act less through extreme gradients and more through sustained exposure to consistent hydrographic, sedimentary regimes and likely finer-scale sediment biogeochemistry and fluxes (Jordà-Molina et al., 2019; Kokarev et al., 2021; Vedenin et al., 2022). This provides important context for interpreting the trait-mediated structuring observed in East Greenland (**I**), where the larger spatial extent and distinct habitat classifications reflect broader-scale environmental filtering, as well as the functional convergence identified along the West Greenland shelf (**II**). Along the warmer West Greenland shelf, elevated temperatures likely strengthen existing environmental constraints, narrowing the viable trait space and reinforcing established filters rather than restructuring the system (Sutton et al., 2021).

This insight is particularly important given that climate change research and associated mitigation narratives frequently place temperature at the centre of ecological explanation and political action (CAFF, 2017; Armstrong McKay et al., 2022; IPCC, 2023). While temperature is a dominant global driver of climate change and an accessible target for policy intervention (Renaud et al., 2008; Armstrong McKay et al., 2022; IPCC, 2023), an exclusive focus on temperature risks obscuring key mechanisms governing benthic productivity and ecosystem functioning (Armitage et al., 2024). The results presented here indicate that, for benthic systems, bathymetry, horizontal currents, oxygen dynamics, salinity regimes, sediment processes, and circulation patterns can exert equal or greater influence on community structure and functioning, and that these variables often covary with temperature in ways that complicate simple attribution. The East Greenland carbon study (**III**) further revealed this, showing that latent variable modelling indicated that steep and complex bathymetry, a common feature of Arctic seascapes due to glaciation events and ice scouring, was associated with elevated benthic biomass. Rather than reflecting temperature or vertical flux alone, these patterns point to the importance of flow–topography interactions, whereby horizontal currents redistribute and concentrate organic material along relief features (Rowe et al., 1994; Pica et al., 2024). In effect, heterogeneous Arctic fjord and shelf systems may function analogously to current-exposed seamounts, where enhanced flow over complex topography sustains disproportionate biomass and biodiversity relative to surrounding sediments (Rowden et al., 2010; Boehlert and Genin, 2013; Kennedy et al., 2025). Such lateral carbon redistribution can intensify benthic carbon processing and retention, with documented sequestration rates in current-accelerated systems reaching one to two orders of magnitude higher than surrounding areas (Barnes & Sands, 2017; Yin et al., 2024). In the context of climate change and policy, horizontal current regimes and benthic communities play a crucial role in regulating the pathways, residence times, and efficiency by which carbon is ultimately sequestered, with benthic productivity hotspots on areas of steep bathymetric profiles potentially representing areas of disproportionate importance (Rowden et al., 2010; Wiedmann et al., 2020; Yin et al., 2024).

There is also the possibility that Arctic benthic communities have been exposed to Atlantic Water conditions for considerably longer than is often assumed. Atlantification of Eurasian Arctic shelves and fjords is not a purely contemporary phenomenon, and historical intrusions of warm Atlantic Water travelling along the seabed may have influenced benthic environments over decadal to centennial timescales (Puerta et al., 2020; Tesi et al., 2021; Gjelstrup et al., 2022). Recognition of the longer-term and subsurface influence of Atlantic Water became increasingly central to the interpretation of this thesis's results. During the early stages of the work, Atlantic Water influence was not an explicit focus, with emphasis instead placed on surface stratification and its implications for carbon flux and benthic communities. Subsequent work on the West Greenland shelf prompted greater consideration of along-shelf currents and advected water masses as structuring drivers, following documentation of Atlantic Water at depth during the ECOTIP expedition aboard *R/V Dana*, 2021 (Munk et al., 2022; Schmidt et al., 2025), confirming and extending earlier hydrographic studies (Curry et al., 2011, 2014; Rysgaard et al., 2020; Mortensen et al., 2022).

Recognition of this hydrographic structure shaped the conceptual framework of Paper **II**, prompting the investigation of how persistent Atlantic Water influence might contribute to the presence of Arctic, Boreal, and Cosmopolitan taxa. Additionally, time-series observations document increased Atlantic Water shoaling on the outflow shelf of Northeast Greenland (Arndt et al., 2015; Gjelstrup et al., 2022), and our data show Atlantic Water close to glacial termini and within fjord basins >76 °N (**III**), even where sills and troughs may partially restrict intrusions (Hill et al., 2017; Bao and Moffat, 2024). Together, these patterns suggest sustained rather than recent exposure to Atlantic Water. If so, benthic communities may already reflect long-term exposure and adaptation to warmer Atlantic conditions, while comparative observations and responses in surface and pelagic systems may appear more rapid because associated stratification and circulation changes are only now being recognised (Carmack et al., 2016; Von Appen et al., 2021; Hordoir et al., 2022). This potential temporal decoupling suggests that benthic responses to Atlantification may reflect prolonged exposure to Atlantic Water conditions, challenging assumptions of novelty and indicating that deep fjord and shelf communities, structured by advected water masses, should be considered separately from shallow coastal, highly flux-driven systems when interpreting species distributions and carbon sequestration.

4.2.2 The significance of trait-mediated structuring of taxa

Trait-based ecology forms the conceptual backbone linking all three Papers, providing a mechanistic explanation for the observed biodiversity patterns. A key insight emerging from this thesis, and one that became fully apparent during the synthesis process, is that traits play a central role in mediating how benthic taxa respond to environmental conditions, thereby structuring community composition and ecosystem functioning across Arctic systems. In Paper **I**, hierarchical modelling revealed that a substantial proportion of among-taxa variation in responses to environmental gradients could be attributed to species traits (γ-$R^2 = 0.53$), indicating that more than half of the variability in environmental responses is explained by functional characteristics rather than species identity alone. In other words, environments do not select species directly; instead, they select for traits, allowing different species with similar functional characteristics to occupy comparable ecological roles (Bremner et al., 2006b; Sutton et al., 2021; Beauchard, 2023) (for a conceptual understanding, see Fig. 11).

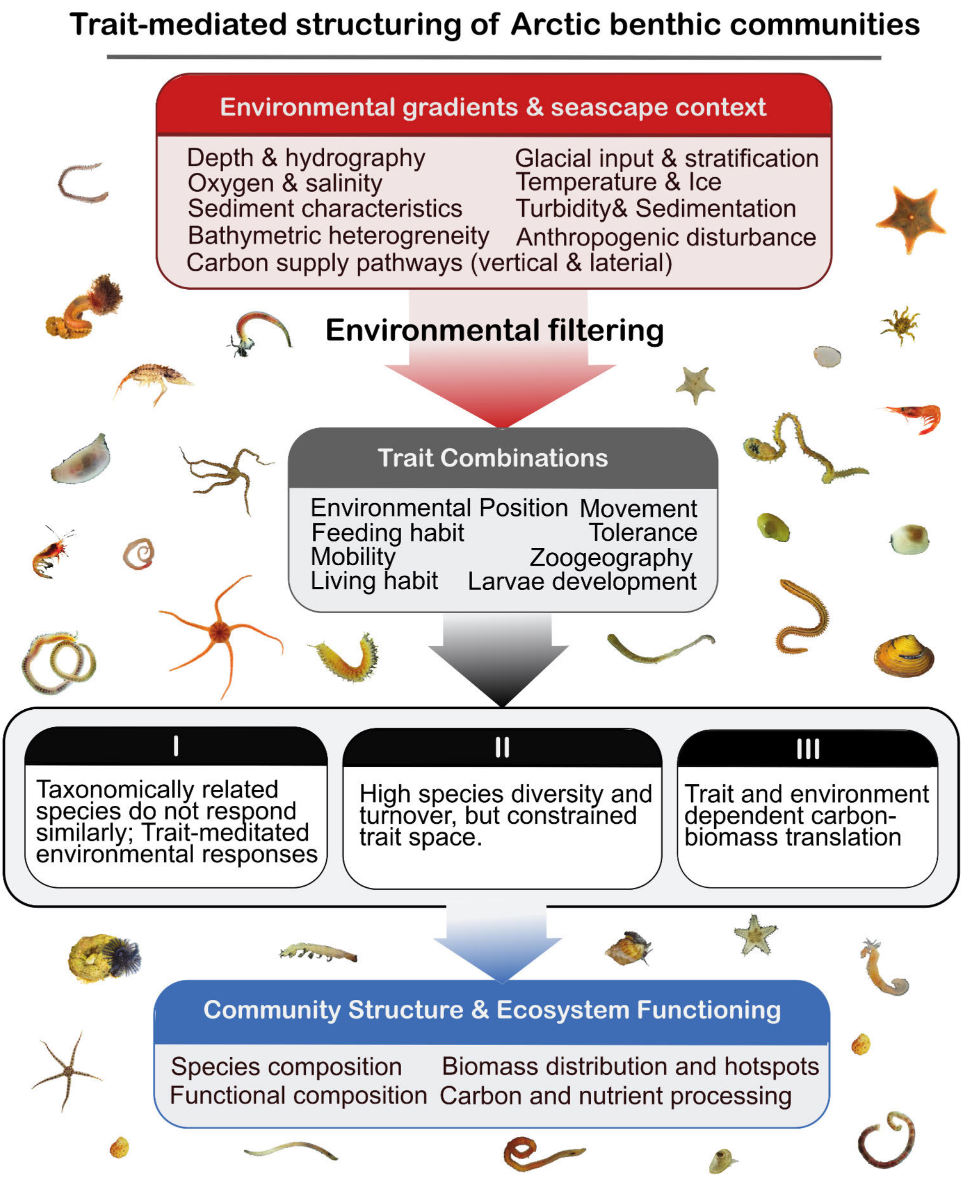


Figure 11. Conceptual framework illustrating trait-mediated structuring of Arctic benthic communities. Environmental gradients and seascape context act through environmental filtering to select functional trait combinations, which mediate community structure and ecosystem functioning. I–III refer to the principal findings of Papers I–III, respectively. Species illustrations are © The Nansen Legacy, 2024.

Table 2. Trait patterns across the three studies and habitat contexts. Trait dominance refers to consistently high contribution to abundance, biomass, or CWM within the specified context.

Trait	Paper	Common trait observations	Overlap / interpretation
Mobility	**I**	Greater evenness in mobile strategies in fjord environments, compared to increased highly mobile strategies on the slope.	**Mobility patterns shift with habitat and biomass context,** but consistently reflect environmental constraints rather than species identity; mixed mobility supports higher biomass under favourable conditions.
	II	Low mobility dominant, followed by none.	
	III	Highly variable across and within systems. Generally, low mobility is associated with reduced community biomass, whereas mixed mobile roles are associated with higher community biomass.	
Adult movement	**I**	Swimmer dominated on the slope, but much more even distribution of movement traits in the fjord.	**Movement strategies track sedimentary and hydrodynamic context,** with burrowing and sessile forms dominant under stable or depositional regimes and a greater functional spread under heterogeneous conditions.
	II	Burrowing dominant, followed by sessile.	
	III	Similar to mobility, highly variable. Generally, sessile & burrowing present in reduced community biomass, and more roles (sessile, burrowing, crawling, etc.) in higher biomass	
Feeding habit	**I**	Most feeding traits are represented in the fjord and shelf, while ~70 % are predators on the slope.	**Feeding mode reflects carbon delivery pathways**: deposit feeding dominates under diffuse supply, whereas suspension feeding increases where advected or downwelling resources enhance pelagic–benthic coupling, supporting a broader range of functional feeding roles.
	II	Deposit, followed by filter/suspension dominant, although filter feeders are variable and sometimes sparse.	
	III	Strong filter feeding and mixed roles at downwelling fjord sites; deposit feeding elsewhere	
Larval development	**I**	Equal representations of development strategies on the fjord and shelf, whereas lecio-trophic strategies declined on the slope	**Development mode varies across habitats but consistently favours direct and planktotrophic strategies,** with lecithotrophic forms reduced in more exposed settings (*e.g.*, slope), suggesting dispersal strategies are structured by hydrographic context and regional connectivity.
	II	Benthic direct development was dominant, although cosmopolitan and boreal taxa sometimes had high affinity for planktotrophic development.	
	III	NA	

Table 2. Continued.

Trait	Paper	Common trait observations	Overlap / interpretation
Reproduction	**I**	Most reproductive traits are represented in the fjord and shelf, while ~70 % are sexual-brooding on the slope.	**Sexual reproductive strategies, particularly external fertilisation and brooding, dominate across habitats**, indicating that life-history mode remains relatively stable across environmental gradients and is less sensitive to local habitat differences than feeding or mobility traits.
	II	Sexual external dominant, followed by sexual-brooding.	
	III	NA	
Living habit	**I**	NA	**Infaunal** strategies (burrowing and tube-dwelling) **dominate in depositional** or sediment-influenced environments, while mixed **epi–infaunal** assemblages are associated with **greater bathymetric complexity and hydrodynamic influence.**
	II	Tube-dwelling (boreal and cosmopolitan taxa) and burrowing (Arctic taxa) are dominant	
	III	Infauna dominated in low biomass, higher sedimentation areas, whereas mixed epifauna and infauna on steep sills	
Tolerance / disturbance	**I**	NA	**High tolerance traits** were prominent in Paper **II**, indicating that in **environmentally constrained** shelf systems, persistent filtering may favour stress-tolerant taxa.
	II	High tolerance dominant	
	III	NA	
Skeleton	**I**	Diverse skeleton structures in the fjord, from calcareous to none, while skeleton type was ≥ 60 % chitinous on the slope.	Skeletal structure was only used in Paper **I,** but the spatial variation likely reflects **habitat-linked environmental selection/pressures**, including substrate type, potential disturbance and predator presence.
	II	NA	
	III	NA	
Zoogeography	**I**	Arctic, boreal and cosmopolitan species are found in the fjord, but with greater Arctic species, whereas the slope is more dominated by cosmopolitan species.	**Taxonomic composition varies regionally, but functional roles converge** across biogeographic groups, supporting the concept of constrained trait space despite species turnover.
	II	Arctic, Boreal, Cosmopolitan ~⅓ each in both species richness and abundance.	
	III	NA	

While trait-mediated environmental filtering is not a new concept in benthic ecology (Pearson and Rosenberg, 1978; Solan et al., 2004; Törnroos and Bonsdorff, 2012), its significance is reinforced by the combined evidence presented across all three Papers. In the Northeast Greenland fjords (**III**), communities were characterised by high benthic biomass and increased filter feeders and other diverse trait roles in areas associated with inferred downwelling and enhanced lateral carbon and nutrient supply. Along the West Greenland shelf (**II**), high species richness and pronounced taxonomic turnover co-occurred with a remarkably consistent trait composition across stations, despite Arctic, Boreal, and Cosmopolitan taxa being present in similar proportions (see Table 2 for full trait comparisons and trends across Papers). Paper **I** therefore provides a mechanistic explanation for the patterns observed across the thesis: species can co-occur or replace one another, provided they share trait combinations that are suited to the prevailing environmental conditions. These constraints are particularly evident with respect to oxygen tolerance, salinity regimes, and sediment-associated processes (**I**), which may act as covariables within broader hydrographic and biogeochemical regimes rather than as isolated drivers (see Section 4.2.2).

Together, these patterns suggest that Arctic benthic communities are structured more by functional compatibility with persistent environmental constraints than by species identity or biogeographic classification. The results presented here suggest that benthic systems around Greenland may be particularly sensitive to trait-mediated filtering, reflecting the physical and biogeochemical constraints characteristic of these environments (Sutton et al., 2021; März et al., 2022). This underscores the necessity of integrating oceanography, sediment dynamics, and benthic ecology through interdisciplinary approaches to accurately assess how seafloor communities respond to change and to evaluate implications for ecosystem services such as fisheries support and carbon sequestration (Solan et al., 2020a).

4.2.3 Biogeography within constrained trait space

A further contribution of this thesis is the clarification of how species from different biogeographic classifications contribute to Arctic benthic ecosystems through their trait composition and associated functional roles. Biogeographical classifications are most informative as indicators of dispersal dynamics and environmental accessibility, shaping which species can enter the system, even if functional organisation is ultimately constrained by trait space. In Paper **II**, Arctic, Boreal, and Cosmopolitan taxa occurred in similar proportions along the West Greenland shelf, with strong station-level turnover. In a transitional region where Arctic and sub-Arctic influences converge, this raises the question of whether the shelf represents a long-standing mixing zone, an actively redistributing system, or a patchwork of environmentally filtered and locally specialised communities, as suggested by the pronounced species turnover between stations. (**II**) (Yesson et al., 2015; Maier et al., 2024). When considered alongside earlier zoogeographic work from Disko Bay and comparisons with other Arctic shelves (Schmid and Piepenburg, 1993), the West Greenland fauna appeared to be dominated by an Arctic-Boreal overlap, with a smaller but persistent Cosmopolitan fraction, in contrast to our recent study of an almost equal representation of Arctic, Boreal, and Cosmopolitan taxa. This pattern of persistent, though generally lower, proportions of cosmopolitan taxa is consistent with assemblages reported from other Arctic regions (Wlodarska-Kowalczuk et al., 2004; Komendić et al., 2024) and suggests that while mixing may be a structural feature of the system, there is still the possibility that cosmopolitan species have increased in species or individual abundance over time and space. This leaves open the possibility of directional biogeographical change in the relative contribution of Cosmopolitan taxa under shifting circulation and habitat conditions, highlighting the importance of improved biogeographic resolution and niche-based analyses to determine whether these taxa represent true generalists or context-dependent specialists.

Paper **I** adds a complementary perspective from Northeast Greenland, where fjord communities were characterised largely by Arctic affinity and traits associated with low mobility and limited dispersal, implying potential sensitivity to rapid environmental change. At the same time, the study provides evidence that responses cannot be inferred from taxonomic relatedness. The lack of consistent responses among phylogenetically related taxa suggests ecological divergence and niche differentiation, indicating that even within Arctic-dominated communities, resilience or vulnerability is unlikely to be uniform across taxonomic groups. Together with the results from West Greenland, these findings refine the interpretation of “range shifts” at the seafloor. Redistribution may be occurring, but its ecological consequences will depend less on whether incoming species are Boreal or Cosmopolitan and more on whether they can occupy, or competitively displace within, the trait space permitted by local environmental conditions. This provides a more process-based framing for anticipating benthic community change, in which biogeography signals opportunities for redistribution, while traits and environmental constraints determine establishment and impact.

4.2.4 Carbon seascapes and potential lateral pathways as drivers of benthic composition and biomass

Arctic benthos are strongly dependent on short, intense seasonal pulses of organic matter following spring and summer production (Clarke, 1983; Griffiths et al., 2017; Wiedmann et al., 2020). In Paper **III**, generalised latent variable modelling revealed that vertical organic carbon flux and benthic organic carbon were associated with responses in benthic biomass, particularly in terms of feeding and mobility traits. Stations characterised by higher flux and sediment carbon supported greater contributions from sessile epifauna and filter or suspension feeders, consistent with a reliance on sustained inputs of labile organic material. However, evidence from polar night studies indicates that benthic biomass and species diversity can remain high outside of peak export periods (*e.g.,* late spring and summer), implying the presence of alternative or sustained carbon pathways (Renaud et al., 2020, and references therein). The high proportions of sessile filter feeders observed in Papers **I** and **III**, taxa that lack the mobility to track episodic food inputs, further suggest that benthic communities may be supported by redistributed or retained carbon sources during periods of reduced vertical flux, or perhaps by specialised biological strategies such as storage or slow growth that allow nutrients acquired during productive periods to be utilised later in the year (a strategy known by kelp; Chapman & Lindley, 1980; Renaud et al., 2020). While the prevalence of such strategies in Arctic benthic fauna remains poorly resolved due to logistical and methodological constraints (*e.g.,* personnel time and costs of research expeditions and laboratory trials), improved species-specific understanding is critical for explaining how benthic communities persist through low-productivity periods and for refining predictions of ecosystem functioning under ongoing environmental change.

In addition to the effects of vertical flux and sediment carbon, further structure in benthic community composition remained that was not explained by the measured carbon variables and may reflect the alternative carbon pathways outlined above. The residual ecological structure, captured by the latent variable in Paper **III**, aligns with slope-driven advection, horizontal transport, and local retention, which shape benthic carbon availability when interpreted in the context of bathymetry and inferred downwelling. Stations scoring high along this latent gradient, associated with steep bathymetry and downwelling conditions, supported the highest benthic biomass, exceeding that of low-scoring stations by more than threefold, and were characterised by elevated contributions of both suspension feeders and mixed feeding taxa. These results suggest that steep sills and downwelling zones act as benthic productivity hotspots, where lateral transport and seafloor morphology amplify carbon or nutrients available beyond what would be predicted from vertical flux alone. In a study by Holtappels et al. (2013), changes in current velocity (2-10 m s^{-1}) in coastal environments can bias vertical flux by 30 – 100 %, further highlighting the discrepancy between carbon and nutrient fluxes derived from downward flux and bottom currents. In this framework, vertical flux serves as the baseline pathway for carbon delivery, while lateral redistribution and seascape structure determine where and how carbon becomes biologically available, thereby shaping both community composition and functional dominance. This perspective refines the assumption that climate-driven stratification will universally weaken pelagic-benthic coupling by reducing carbon delivery to the seafloor, but more importantly, highlights how lateral transport and local retention can reorganise carbon availability in space and time.

Collectively, the Papers show that benthic community structure around Greenland reflects sustained environmental constraints acting through functional trait space, rather than simple temperature-driven or taxonomic shifts. Differences among fjord, shelf, and slope environments emerge from variation in hydrography, sedimentation regimes, oxygen dynamics, and carbon redistribution, yet within each system, trait compatibility determines which species establish, persist, and contribute to biomass. High species turnover can therefore occur without major shifts in functional organisation, while biomass hotspots arise where hydrographic forcing and seafloor morphology enhance carbon availability beyond vertical flux alone. This integrated seascape perspective, linking environmental gradients, trait-mediated filtering, biogeographic overlap, and carbon pathways, provides a mechanistic framework for understanding Arctic benthic ecosystem structure and functioning under ongoing environmental change (Fig. 12).

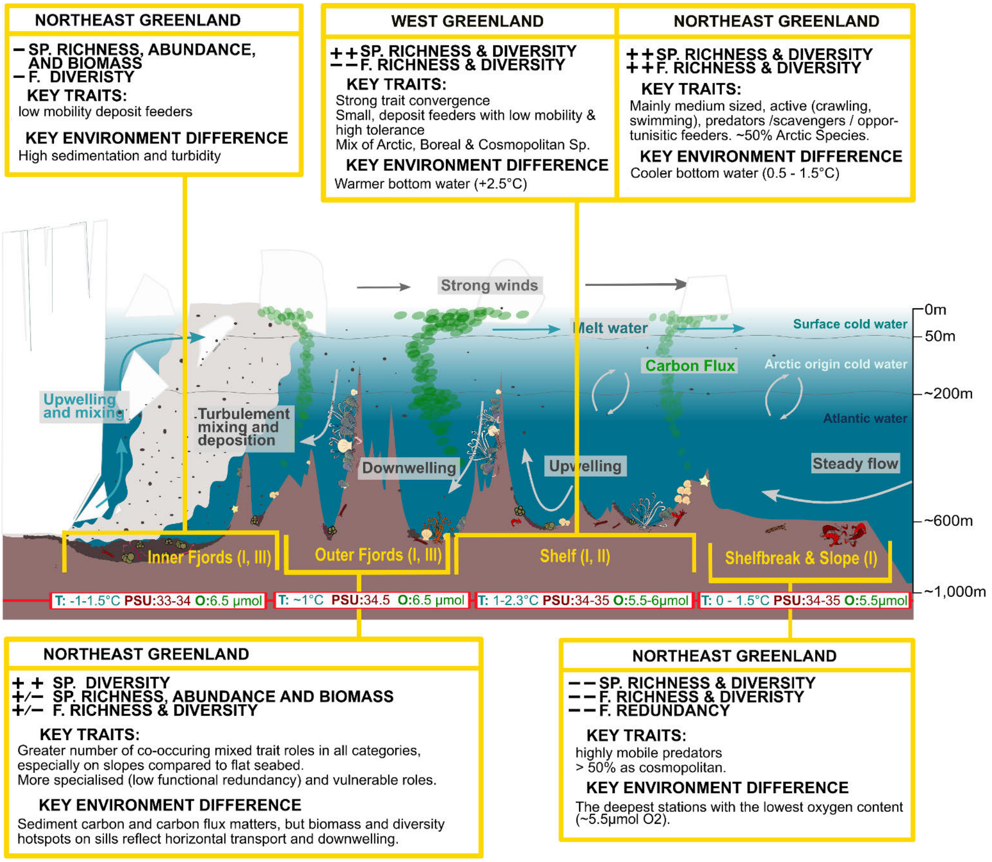


Figure 12. Conceptual figure of the synthesised results showing differences in communities and drivers in relation to the results of each Paper. Key for boxes: SP = Species, F = Functional, ++ = very high, + = high, +/- =both high and low, - = low, and -- = very low. Environmental gradients are shown for each habitat in red boxes along the bottom with T = Temperature, PSU = Salinity, and O = Oxygen.

4.3 Limitations and personal reflections

This thesis primarily uses species traits to examine how environmental gradients structure functional composition, revealing high taxonomic turnover alongside constrained trait distributions, rather than focusing on individual species. While this trait perspective departs from more traditional benthic community research, it is now widely recognised that trait-based perspectives are just as important as species-based approaches, particularly in the context of a rapidly changing world (Degen et al., 2018; De Juan et al., 2022; Vivó-Pons et al., 2023; Susini et al., 2025). When viewed across multiple temporal scales, change is a universal constant, and benthic species assemblages are no exception; although rare examples of long-term evolutionary stasis have been documented, such as in ancient ray-finned fish lineages including gars and sturgeons, most taxa undergo continual evolutionary change (Brownstein et al., 2024). Yet, the functions organisms perform, how they interact with their environment, and the ecological roles they fulfil may be conserved even as species composition shifts.

I further argue that advancing trait-based research and understanding the function of organisms is highly relevant in light of current societal and ecological challenges, including carbon cycling, habitat restoration, biodiversity conservation, and sustainable fisheries. An analogy can be drawn with organisational systems, where retaining individuals who perform key functions is often prioritised over maintaining roles that no longer contribute meaningfully to system performance. In an ecological context, this highlights the importance of identifying species whose traits underpin critical ecosystem processes, particularly where management and conservation efforts aim to safeguard or enhance specific functions and services. Importantly, this does not imply support for species loss or extinction. It is well recognised that rare species may play important ecological roles that can be overlooked, particularly when analyses focus on abundant taxa with well-characterised traits (Törnroos et al., 2015; Säterberg et al., 2019; Palummo et al., 2025). Rather, I view this as an argument for further development of trait-based frameworks, which would enable a better understanding and quantification of the contributions of rare species and less obvious ecological functions given the complexity of ecological interactions.

This work relied on expedition-based sampling rather than laboratory experiments, meaning that many environmental variables could not be controlled. For example, during the RV *Maria S. Merian* cruise in Northeast Greenland, the ADCP could not be used to measure near-seafloor current flow because it had to be removed for microplastic sampling. This information would have been valuable for testing whether downwelling and current speed contributed to the higher benthic invertebrate abundance and biomass observed on steep sills (**III**). Yet this interdisciplinary sharing of resources (microplastic research alongside benthos and other research) is also a key consideration when participating in large consortia. While being part of a consortium enables access to costly and logistically complex expeditions, it can also constrain sampling design by 1) predetermined sampling locations and frequencies, and 2) having a small number of replicates across stations separated by large spatial distances. These constraints make it difficult to implement advanced statistical approaches and draw strong conclusions about ecological similarities, differences, and underlying mechanisms; an outcome that is more easily achieved when surveying an area at high resolution, with the ability to recollect data as desired.

Throughout the PhD, there were repeated discussions about whether to restrict analyses to fewer coastal systems or stations in order to increase the study's resolution. While such an approach may yield detailed insights at smaller scales, discarding large portions of data felt challenging, given the cost, effort, and rarity of Arctic benthic observations. Reducing the dataset also risked overlooking broader-scale patterns, including the key finding that was revealed through the latent variable approach in Paper **III**. Ultimately, I am satisfied with how the studies developed, and with the meaningful contribution they make to our understanding of Greenland and Arctic marine ecosystems. I hope that these results will be built upon and expanded upon in future research.

Final comment on the environmental state: The shift from one stable environmental state to another is often referred to as an ecological tipping point, and evidence of these shifts already occurring in the Arctic is the premise of one of the EU Horizon 2020 project, that this work is part of (Investigating Ecosystem Tipping Points and Cascades in the Arctic Seas (ECOTIP), 2020-2024). While temperatures continue to increase globally, as shown by long-term time series data (Armstrong McKay et al., 2022; Rantanen et al., 2022; IPCC, 2023), the Arctic is not yet in a new stable state with large annual variations in sea ice and both air and sea temperatures (Crow and Prange, 2025). The region has also been described as a comparatively young marine environment (Clarke, 1983), underscoring its inherent dynamism. Thus, we should reflect on the fact that this work was developed and conducted within the “hysteresis” stage of a tipping point, an uncertain and evolving period where frameworks and theoretical models are constantly being revised and adapted. In this context, our aims, data collection, and emerging results should not be seen as fixed conclusions but rather as part of an ongoing, adaptive process of interpretation shaped by state-of-the-art knowledge and the shifting nature of Arctic (and other) marine ecosystems in light of climate change. While the nature of the thesis's data collection can only provide a ‘snapshot’ in time, there is a fair amount of information to be learned and ecological interpretation to be given, allowing the next generation of scientists to build on it.

5. CONCLUSIONS

5.1 Key findings and implications

This thesis examines macrobenthic invertebrate communities around Greenland to improve understanding of how Arctic benthic ecosystems are structured and function under ongoing environmental change. By focusing on fjord, shelf, shelf break, and slope habitats, it addresses systems exposed to multiple interacting pressures, including declining sea ice, increased sedimentation and turbidity, expanding human activities, and changes in water column structure, notably the influence of warmer Atlantic-derived waters at depth.

Rather than focusing on species identity alone, this work adopts a trait-based perspective to evaluate how benthic organisms interact with their environment, how functionally diverse or constrained communities are, and what these patterns imply for ecosystem functioning. This approach is particularly informative in Arctic systems, where changes in species composition do not necessarily translate into immediate functional change, and where traits provide a mechanistic framework for interpreting benthic responses to environmental filtering. With that, the thesis summary provides three overarching take-home outcomes:

Environmental filtering structures benthic functioning across Greenlandic seascapes. Across fjord-to-slope systems, benthic communities differed in both taxonomic and trait composition, indicating consistent environmental filtering across larger spatial scales. Trait-based analyses showed that community structure responds to composite environmental regimes, linking functional composition to gradients in depth, sediment characteristics, hydrography, and spatial context rather than single drivers. These results provide an important trait-based baseline for Arctic benthic ecosystems, particularly in Northeast Greenland, and demonstrate the value of functional approaches for understanding seafloor biodiversity beyond species identity.

Biogeographic overlap with strong functional convergence on the West Greenland shelf. Arctic, Boreal, and Cosmopolitan taxa co-occurred along the West Greenland shelf, consistent with a long-standing biogeographic mixing zone, yet communities showed pronounced convergence in trait composition across taxa of different origins. Despite modest environmental variability and slightly elevated bottom temperatures compared to Northeast Greenland, communities occupied a narrow functional space, indicating strong environmental filtering acting on traits rather than species identity and suggesting that additional, potentially cumulative pressures may be constraining functional roles. This functional convergence raises important questions about long-term implications for ecosystem resilience, trophic interactions, and fisheries productivity.

Trait-mediated links between carbon supply, bathymetry, and benthic productivity. Snapshot observations and trait-based analyses revealed that vertical carbon flux primarily supports sessile suspension feeders, while interactions between flux and sediment carbon sustain mixed feeding strategies, linking benthic biomass to carbon delivery pathways. Predatory taxa were most abundant in areas of high overall benthic biomass, likely reflecting secondary responses to enhanced prey availability. Most notably, the highest benthic biomass and trait diversity were associated with steep bathymetric features, where biomass was up to three times higher than in near-glacial stations, highlighting the importance of horizontal currents and the lateral redistribution of carbon and nutrients. These benthic productivity hotspots likely represent areas of disproportionate ecological and biogeochemical importance across Arctic fjord and shelf systems, processes that are often overlooked relative to vertical flux but appear critical for sustaining benthic productivity.

Overall, this thesis demonstrates that Arctic benthic ecosystems around Greenland are structured by persistent environmental filtering that acts primarily through biological traits, shaping community composition, functional convergence/divergence, and carbon-related ecosystem processes. The possibility that benthic communities have experienced long-term exposure to Atlantic-derived water masses challenges assumptions of purely recent change and underscores the need to distinguish between long-standing environmental constraints and emerging pressures. Future conservation and management efforts will benefit from moving beyond temperature-centric perspectives to incorporate trait-based ecology, seafloor morphology, and lateral carbon pathways. Such integrative approaches are essential for anticipating ecosystem responses, identifying functionally important habitats, and safeguarding the role of Arctic benthos in supporting biodiversity, fisheries, and long-term carbon storage in a rapidly changing Arctic.

5.2 Future recommendations and research

This thesis presents a snapshot of Arctic benthic systems during a transitional period characterised by environmental instability and emerging tipping-point dynamics. As such, several avenues for future research are apparent.

First, expanding spatial and temporal coverage is essential. Long-term monitoring and repeated sampling across seasons and years would enable assessment of whether the observed patterns persist, intensify, or shift as Arctic climate change progresses. In particular, coupling trait-based benthic data with continuous measurements of water-column processes, including near-bottom currents and downward and lateral particle flux, would strengthen mechanistic understanding of pelagic-benthic interactions.

Second, further development of trait frameworks is needed, particularly with respect to rare and poorly characterised species. While dominant taxa often drive ecosystem processes, the datasets in this work were largely made up of rare species, which may contribute unique or context-dependent functions that remain underrepresented in current trait databases. This also applies to intraspecific variability and continuous traits, which remain poorly resolved in current trait frameworks despite their potential importance for capturing context-dependent responses to environmental change (Williams et al., 2025). Improving trait resolution for these taxa would enhance the ability of functional approaches to capture the full spectrum and weight of benthic ecosystem roles.

Third, integrating functional benthic indicators into ecosystem-based management and conservation strategies represents an important future direction. Trait-based metrics have clear potential for assessing habitat condition, functional redundancy, and ecosystem resilience, particularly in data-limited regions such as the Arctic. Linking these metrics to management objectives related to carbon cycling, habitat restoration, and fisheries sustainability would increase their applied relevance.

Fourth, greater cross-disciplinary collaboration is essential for advancing understanding of benthic ecosystem functioning. Stronger integration between pelagic and benthic research, and across paleo benthic, geochemical, physical, morphological, ecological, and biological approaches, would substantially improve assessments of benthic carbon pathways. Paper **III** demonstrates the value of combining sediment trap flux data with high-resolution bathymetric information, such as multibeam-derived seafloor morphology, to reveal patterns that would not be apparent from single data streams alone. Wider adoption of such integrative approaches, supported by collaborative frameworks and shared analytical capacity, is likely to be crucial for enhancing the understanding of benthos and their roles, not only in carbon sequestration but also in fisheries productivity and other key ecosystem services.

Ultimately, this work highlights the importance of considering Arctic benthic ecosystems as dynamic systems operating within an evolving environmental context. As the Arctic continues to move through the hysteresis phase of a broader climatic and ecological tipping point, adaptive frameworks that combine functional ecology, long-term observations, and flexible modelling approaches will be critical. The results presented here provide a foundation for such efforts and offer a baseline against which future change can be evaluated.

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Ort och tid/Place and time

Turku/Åbo Wednesday, 17 June 2026

Underskrift/Signed by

Phoebe Armitage

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ECOTIP: Investigating Ecological Tipping Cascades in the Arctic Seas

This Ph.D. research was funded by the European Union's Horizon 2020 research and innovation programme under Grant Agreement No. 869383 and forms part of the ECOTIP project, *Investigating Ecological Tipping Cascades in the Arctic Seas* (2020–2024). ECOTIP brought together 15 research institutes across Europe and Japan to investigate ecological tipping points and cascading responses in Arctic marine biodiversity under rapid environmental change. A central objective of the project was to assess how shifts in biodiversity influence ecosystem functioning using trait-based approaches, with particular emphasis on pelagic-benthic coupling and implications for fisheries and carbon sequestration.

SEA-Quester: Marine Carbon Cycling in Emerging Polar Ecosystems

This Ph.D. research has also been supported by the European Union's Horizon Europe programme through the SEA-Quester project (Grant Agreement No. 101136480; 2024–2028). SEA-Quester investigates marine carbon cycling in emerging polar ecosystems shaped by climate-driven reductions in sea ice, altered circulation patterns, and ocean warming. The project examines how these changes affect species distributions, biological processes, ecosystem functioning, and carbon sequestration potential in the polar seas. As a successor to ECOTIP, SEA-Quester brings together a European consortium to evaluate the implications for biodiversity conservation and climate-mitigation targets, with a focus on ecosystem services related to carbon storage and processing.

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Paper I

Diverging benthic trait diversity and drivers across fjord to slope habitats of the high Arctic

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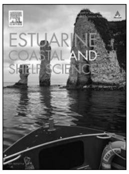

Diverging benthic trait diversity and drivers across fjord to slope habitats of the high Arctic

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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 (ºC), 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 R3 Sexual: brooding R4 Sexual: internal	Food availability to the benthic/pelagic realm, resource facilitation, carbon transportation, and dispersion and recovery capabilities.	Asexual reproduction can occur because of 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

(*continued on next page*)

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 – λ) 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

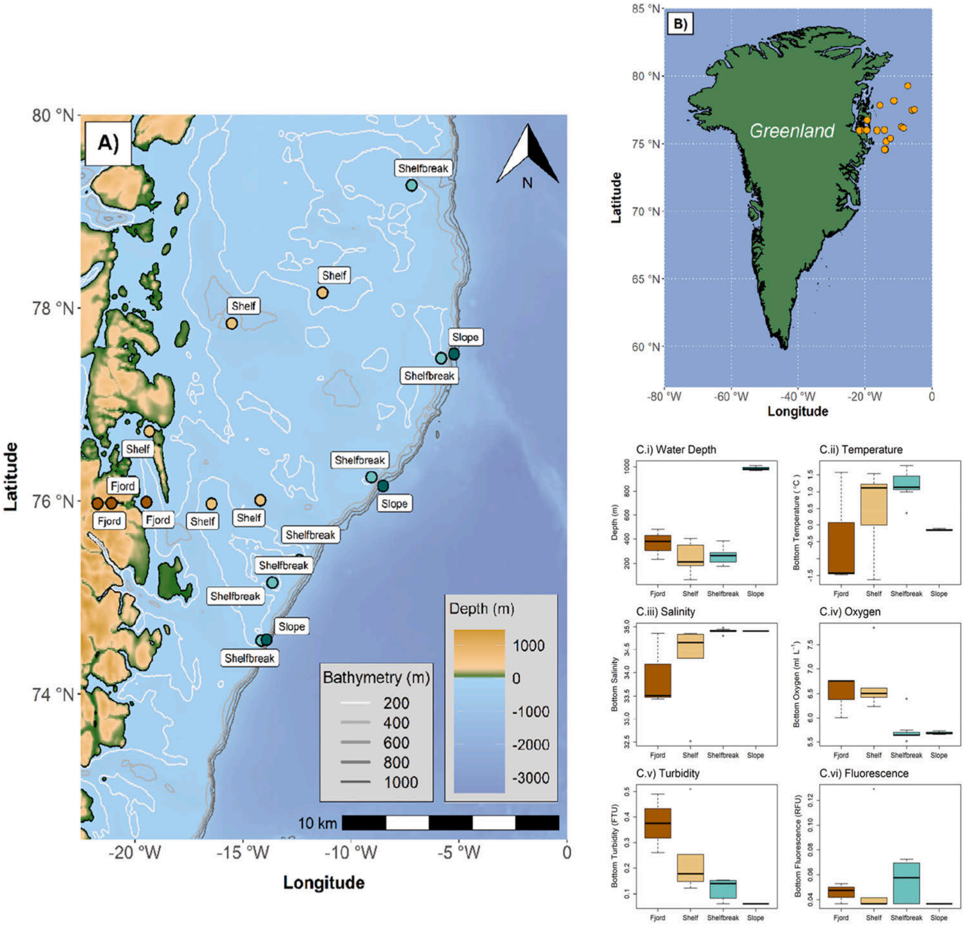


Fig. 1. Study area. A) Map of the 18 stations sampled across the Northeast Greenland Shelf. Contour lines represent bathymetry up to 1000m, and B) overview of Greenland and the location of the respective stations, and C) environmental variables used in the analyses including i) water depth (m), ii) bottom 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

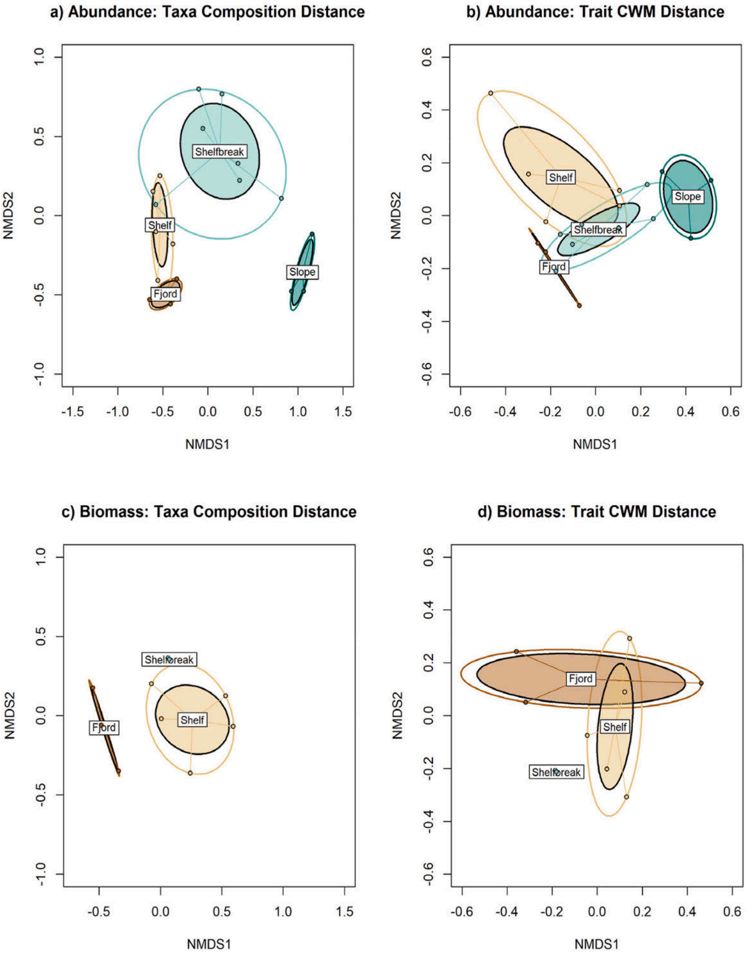


Fig. 2. Dissimilarities are shown between habitat groups (fjord, shelf, shelf-break, and slope) of epibenthic communities and their trait group assemblages. a) and b) show the dissimilarities in taxa and trait communities from the abundance data (number of individuals 1000 m^{-2}), while c) and d) show 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).

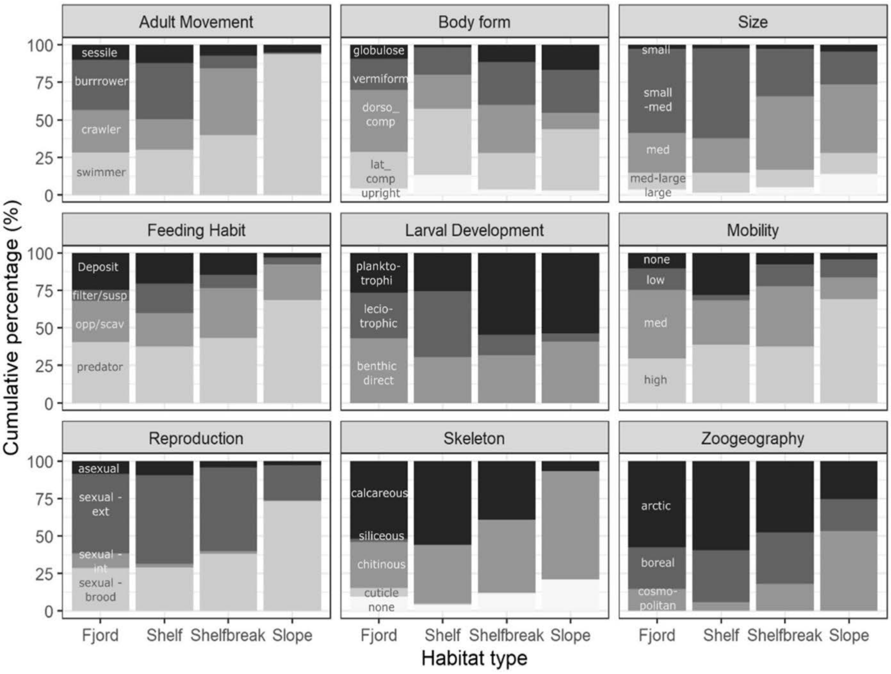
and shelf groups (Fig. 4b). Taxa diversity was high across the fjord (mean Simpson Index ± SD = 0.76 ± 0.09, shelf (0.68 ± 0.27), and shelf-break (0.78 ± 0.15), with the lowest diversity occurring in the slope region (0.47 ± 0.22). This trend was similarly found for taxa vulnerability, although variability 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 predominately 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

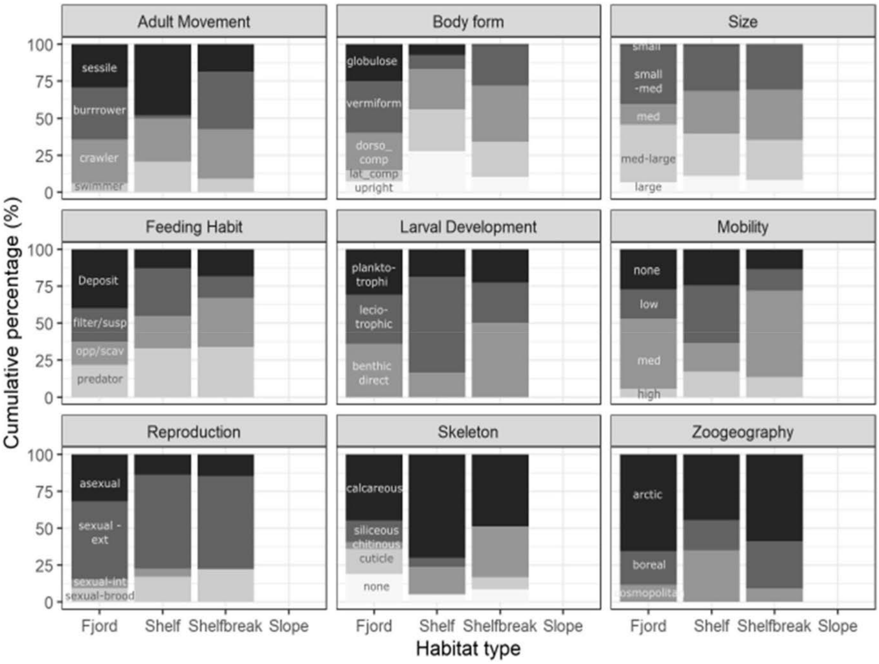


Fig. 3. Community-weighted mean (CWM) values of exhibited traits for a) abundance and b) biomass data were converted into the cumulative percentages for each habitat type (fjord, shelf, shelf-break, and slope). See Table 1 for trait definitions.

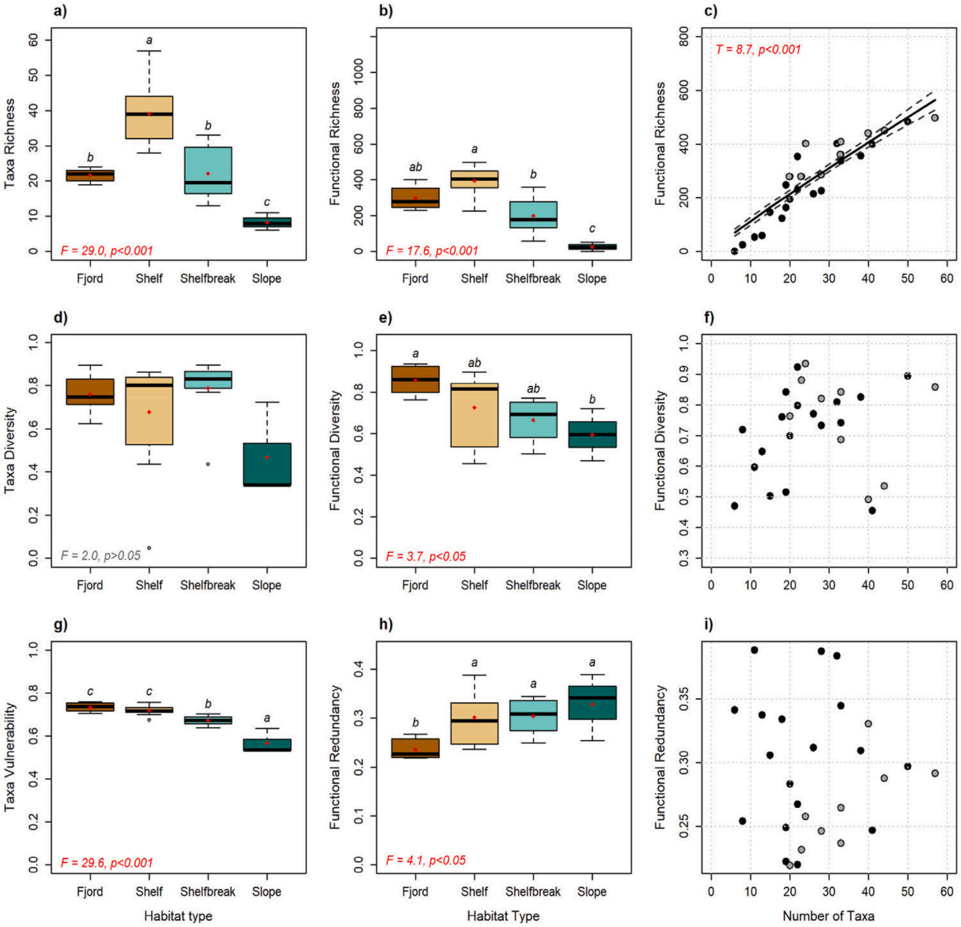


Fig. 4. Biodiversity and functional indices of the Northeast Greenland coast. Plots a), b), d), e), g), and h) show taxa or functional index and the relationship over habitats. Plots c), f), and i) display a functional index against the number of taxa. Functional Diversity is equal to Functional Divergence 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 $(\Pr(\rho > 0) = 0.58; \mathrm{E}(\rho = 0.18))$ (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

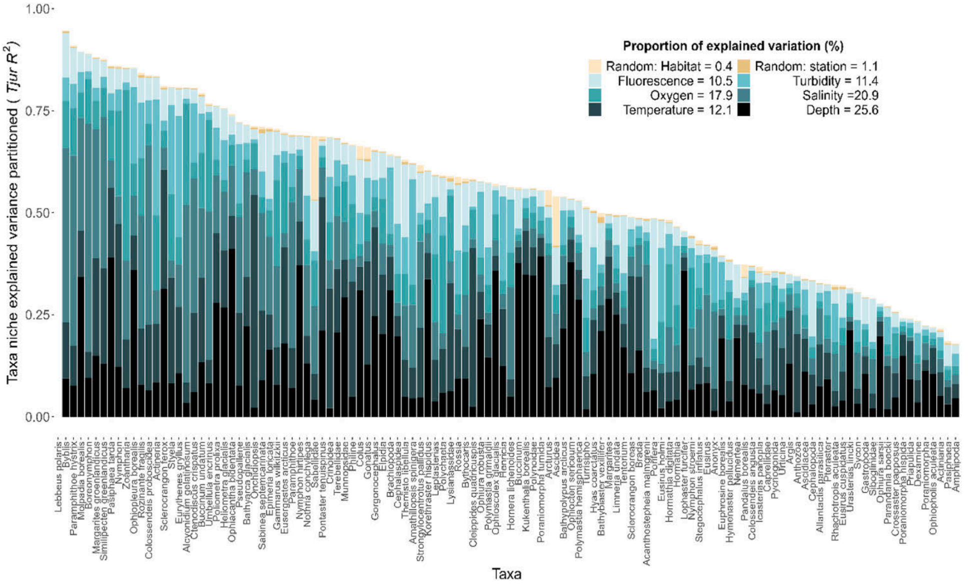


Fig. 5. Total explained variations (*Tjur* R^2) of species occurrences partitioned into responses to fixed (blue coloured bars) and random effects (beige bars). Taxa are ordered by decreasing explanatory power. The bar plot shows species-specific results while the legend indicates the averages of the 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

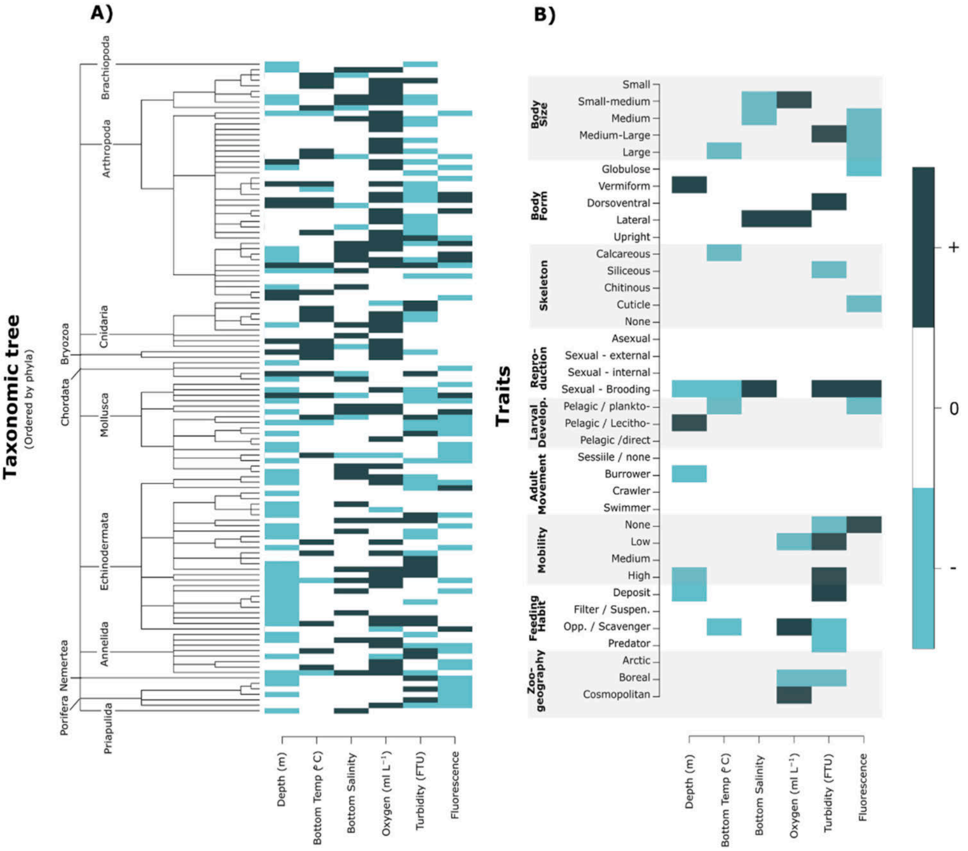


Fig. 6. Linear relationships of A) taxa responses to the environment and B) trait responses to the environment. For A), taxa are ordered according to their taxonomy and illustrated as a taxonomic tree. Phyla names are included at the branch root. In A) and B), taxa and trait responses are shown as positive (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, Methodology, 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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Paper II

Biogeographic diversity meets functional similarity: Trait convergence in benthic infauna from the Arctic ice-covered North to ice-free South

Diversity and Distributions

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Diversity and Distributions

RESEARCH ARTICLE OPEN ACCESS

Biogeographic Diversity Meets Functional Similarity: Trait Convergence in Benthic Infauna From the Arctic Ice-Covered North to Ice-Free South

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ABSTRACT

Aims: Species redistributions and ecological shifts are increasingly evident in Arctic ecosystems, but few studies have examined benthic invertebrate communities using biogeographic and functional frameworks. This study examines the distribution of Arctic, Boreal, and Cosmopolitan infaunal species across a latitudinal gradient on the West Greenland shelf, and whether these distributions are influenced by environmental drivers and trait-based strategies.

Location: West Greenland Shelf, from Nuuk to Disko Bay.

Methods: We analysed abundance and trait data for 161 benthic taxa across nine stations. Biogeographies were assigned at the species or genus level, and β-diversity was decomposed into turnover and nestedness components. Environmental gradients were characterised using PCA of sediment properties, water mass characteristics, and spatial variables. Multiple Regression on distance Matrices (MRM) assessed how these gradients explained variation in taxonomic and trait composition.

Results: Species richness was almost evenly split among Arctic, Boreal, and Cosmopolitan groups, with no clear latitudinal gradient. High β-diversity was driven by turnover, yet trait-based analyses revealed low functional diversity and convergence across all three biogeographic groups, dominated by low mobility and deposit feeding. Cosmopolitan and Boreal taxa were more strongly associated with water mass and spatial gradients than Arctic taxa, consistent with broader dispersal abilities. Arctic taxa showed weaker model fits, likely due to patchier distributions, with environmental associations only evident in composite models rather than as individual predictors.

Main Conclusions: The West Greenland shelf supports a taxonomically diverse but functionally constrained benthic community, characterised by an even contribution of biogeographic groups. Community assembly is not random but shaped by spatial and environmental gradients across broad temporal and geographic scales. These findings underscore the importance of integrating trait and biogeographic data to identify signs of community reorganisation and to inform conservation efforts aimed at maintaining functional diversity and resilience in Arctic shelf ecosystems, extending beyond species identity.

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1 | Introduction

Recent scientific literature increasingly documents species redistributions and ecological transitions in the Arctic, linked to rapid warming, diminishing sea ice, and shifts in ocean circulation patterns (IPCC 2019; Rantanen et al. 2022; Kim et al. 2023). On the West Greenland Shelf, the influence of Atlantic water, carrying warmer temperatures and higher nutrient content, has become increasingly pronounced (Gjelstrup et al. 2022; Rysgaard et al. 2020; Schmidt et al. 2025). This region is shaped by the interaction of the West Greenland Coastal Current (a mix of warm Atlantic and cold Arctic water masses), the West Greenland Current along the slope (warm, saline Atlantic water), and inflows from Baffin Bay (cold, fresh water from the Canadian Arctic), creating a mosaic of overlapping water masses (Curry et al. 2014; Rysgaard et al. 2020). Together with complex seafloor topography and heterogeneous sediments, these interacting currents create dynamic habitats that structure benthic persistence and productivity (Curry et al. 2011; Degen et al. 2016; Bluhm et al. 2020). Such circulation not only modifies local conditions but may also facilitate the movement of species across traditional biogeographic boundaries, enabling the coexistence of taxa with contrasting life-history strategies (Wisz et al. 2015; Csapó et al. 2021). These processes raise critical questions about species competition, functional diversity, and food web stability, posing complications for marine conservation and management. For example: Are potential newcomers opportunistic or specialist species, and would they enhance (or disrupt) native ecosystem functioning or resilience? Evidence from other warming systems (Kortsch et al. 2012; Frainer et al. 2017; Kuletz et al. 2024) suggests both outcomes are possible, but the Arctic remains a frontier where long-term impacts are still largely unknown as well as highly context- and region-specific.

Despite numerous studies documenting distributional shifts across a wide range of Arctic taxa, from zooplankton to marine mammals (Richardson 2008; Heide-Jørgensen et al. 2022; Kuletz et al. 2024), benthic invertebrate communities remain markedly understudied, with relatively more attention given to epifauna (living on top of sediments) than to infauna (living within sediments) (Yesson et al. 2015; Maier et al. 2024). Consequently, our understanding of infaunal geographic distributions and environmental responses in the Arctic remains limited (Wiedmann et al. 2020). Yet, infauna plays a pivotal role in mediating biogeochemical fluxes, organic matter processing, and benthic–pelagic coupling and serves as an essential link in high-latitude food webs (Kortsch et al. 2015; Frainer et al. 2017; Griffiths et al. 2017). Native Arctic species often have relatively restricted dispersal capacities and specialised life-history strategies, which further underscores their vulnerability to climate-induced habitat changes (Pechenik 1999; Meyer et al. 2017; Meyer-Kaiser et al. 2022; Maier et al. 2024).

In dynamic systems such as Arctic marine shelves, assessing what an organism does by its traits offers a robust means to evaluate the consequences of species turnover, not only by identifying which species are gained or lost, but also by elucidating the ecological functions they perform (Bremner et al. 2006; Beauchard et al. 2017; de Juan et al. 2022). In this context, changes in community composition can arise through turnover, referring to the replacement or substitution of species or traits across space or time, or through nestedness, where communities differ primarily through the loss or gain of species or traits from a shared pool. These compositional changes matter because functional performance emerges from morphological or biological traits, such as mobility, feeding mode, and reproductive strategy, which determine how organisms interact with their environment and thereby influence ecosystem functioning (Violle et al. 2007; Solan et al. 2008; Degen et al. 2018). Species traits can effectively predict ecological vulnerability and resilience across diverse systems (Gagic et al. 2015; Törnroos et al. 2015). Thus, the practice of monitoring trait community composition can highlight early changes in critical ecosystem-level processes such as nutrient cycling, sediment stability, and secondary production (Queirós et al. 2014; Degen et al. 2016; Solan et al. 2020), particularly when used to evaluate the impact of species turnover over varying spatial and temporal scales (Frainer et al. 2017).

In this study, we examine benthic infaunal invertebrate communities along a latitudinal gradient from Disko Bay in the north (~70° N), characterised by seasonal ice cover and strong Arctic influence, to the ice-free, temperate waters near Nuuk in the south (~64° N), crossing the Arctic Circle line of latitude (66°33′ N). For species biogeographic affiliations, we classify taxa into Arctic, Boreal, and Cosmopolitan groups to highlight their distributions along the shelf and detect novel or convergent community-level traits that might influence ecosystem functioning. Additionally, we compare traits associated with dispersal and resource strategies among these groups to highlight (if any) key strategies that might differ among them (e.g., r- vs. k-strategist traits, including high (or low) fecundity and broad (or limited) dispersal). We then integrate species abundance data with trait-based analyses to assess how community and trait composition (including the degree of turnover vs. nestedness), and species and functional diversity, vary across gradients of latitude, ice cover, sediment characteristics, and water-mass properties. As these gradients may act independently or interactively, we employ a dissimilarity-modelling framework to disentangle the key abiotic drivers structuring benthic community assembly, examining both individual variables and their combined effects.

Together, these aims seek to address three overarching research questions. First, we ask how Arctic, Boreal, and Cosmopolitan taxa are distributed across the shelf and whether their relative contributions change with latitude. We hypothesise that Cosmopolitan and Boreal taxa occur throughout the gradient due to the long-term influence of Atlantic-derived bottom waters but decline in relative importance northward as Arctic taxa become more dominant. Second, we assess whether spatial turnover in species composition is accompanied by corresponding changes in trait composition. We hypothesise that high species turnover among stations leads to more diverse trait strategies across space, reflecting variation in environmental conditions and habitat structure. Third, we test which environmental gradients structure species and trait composition. We hypothesise that distinct environmental gradients drive trends in species composition and trait expression. For example, sediment characteristics and organic content may favour burrowing and deposit-feeding strategies; hydrographic gradients, such as depth and currents, may favour suspension feeders and taxa with pelagic larvae stages; and spatial–climatic gradients related to sea ice and latitude may favour Arctic-affiliated species. Together, these hypotheses provide a framework for evaluating how environmental filtering, dispersal processes, and biogeographic history interact to shape benthic community structure and functioning along an Arctic shelf gradient.

2 | Material and Methods

2.1 | Study Area

Data collection was conducted along the West Greenland Shelf between latitudes of 64° N (Nuuk) and 71° N (Disko Bay) on board R/V Dana (Institute for Aquatic Resources, Technical University of Denmark) as part of the Horizon 2020 project ECOTIP in July, 2021 (Munk et al. 2022) (Figure 1). The shelf, ca. 2000 km long and 40–250 km wide, connects to Baffin Bay, Davis Strait, and the Labrador Sea. Several shallow sills and banks (e.g., Hellefiske, Fyllas) enhance productivity through upwelling and mixing (Josefson and Mokievsky 2013), making the region ecologically and economically significant (Munk et al. 2022). Fjords and glaciers contribute sediment and freshwater, including the Jakobshavn Glacier, one of the world's fastest-moving tidewater glaciers, which strongly influences Disko Bay hydrography. Sea ice forms in autumn and persists through spring in the northern shelf, while areas south of Maniitsoq (~148 km north of Nuuk) remain ice-free year-round (Figure 1). Depths at study sites ranged 120–740 m, with substrates of soft mud to muddy sand/gravel.

2.2 | Macrofauna Sampling

Macrobenthic invertebrates were collected using a standard box core (sampling area 1000 cm^2; 40 × 37 × 56 cm), sieved through 1 mm mesh, and preserved in 70% ethanol for further sorting and processing and taxonomic identification. A 1 mm mesh was used to reflect the spatial scale of the 1 m^2 box-corer and to capture broad patterns in community structure, acknowledging that smaller-bodied taxa may be underrepresented and that this choice may influence diversity estimates. In total, 32 samples were taken from 10 stations; one hard-bottomed station (cruise station no. 26) with over 1000 brittle stars was excluded. The remaining 9 stations were renamed 1 (south)—9 (north), of which 7 stations had 3 replicates and 2 stations had 2 replicates. The stations spanned the shelf in latitudinal order, including two in Disko Bay near the Ilulissat Icefjord. Organisms were sorted, taxonomically identified, and counted, and densities standardised to individuals m^{-2}. A further square-root transformation was applied to minimise outliers (station range prior to transformation = 0–256 individuals in abundance).

2.3 | Defining Species Biogeographic Affiliations

Climate models project that the geographic and climatic criteria defining the Arctic (e.g., July 10°C isotherm, perennial sea ice, treeline, permafrost) may shift markedly within the next 30 years (Wang and Overland 2009; Kim et al. 2023). Thus, using the Arctic Circle definition of the Arctic, and since our study was conducted while ice conditions and the July 10°C isotherm are still present, our study area provides a baseline "snapshot" of current community structure and trait distributions, contextualised by species' biogeographic affiliations.

To distinguish between Arctic, Boreal, and Cosmopolitan species, we combined trait-based and occurrence-based information. The Arctic Traits Database (https://arctictraits.univie.ac.at/) provides biogeographic assignments for most taxa, although often with limited references. However, occurrence data can be biased by factors such as sampling effort (e.g., research interests, access to sites, frequency of sampling, and time of year). We therefore integrated both sources. We conducted a search for species occurrences, first restricted to species and genus levels to reduce Cosmopolitan bias, using a combination of the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/), Ocean Biodiversity Information System (OBIS; https://obis.org/) and the World Registry of Marine Species (WoRMS; https://www.marinespecies.org/). Following taxonomic screening, the dataset was reduced from 244 taxa to 161 (121 species and 40 genera). Excluded records included indeterminate taxa (e.g., unidentified taxa or colour morphs), non-benthic organisms (e.g., fish or algae), records identified only to higher taxonomic levels (above the genus level), and duplicate or synonymous taxonomic entries resulting from updated taxonomy. Taxa are hereafter referred to as "species".

Using R software (version 2024.09.1; package "robis", Provoost et al. 2022), the latitude and longitude were extracted for every global occurrence for each species. Latitudinal breakpoints were then defined to classify Arctic (−90° to −65° S & 65° to 90° N), Boreal (−65° to −50° S & 50° to 65° N), and Cosmopolitan species (−50° S to 50° N). A species was assigned to a group if > 60% of its records fell within the corresponding range. The > 60% threshold was selected to identify the dominant biogeographic affinity of each species, ensuring that assignments reflected a clear predominance of occurrences within a given latitudinal zone while allowing for species with broad or multi-regional distributions. Importantly, the Arctic group included species with distributions spanning both high-latitude hemispheres (i.e., Arctic and Antarctic). Excluding the Southern Hemisphere would have removed species occurring in roughly equal proportions at both poles, even though their distributions suggest they are more closely aligned with polar environments than with Boreal or Cosmopolitan environments. We therefore retain these species within the Arctic category, while noting that some are not restricted to the Arctic alone. Results were compared against the Arctic Trait Database, GBIF, OBIS, and WoRMS, and the species biogeographies were determined based on these components (frequency at latitude, trait definition, and expert knowledge). Species abundance patterns within Arctic, Boreal, and Cosmopolitan groups were visualised using heat maps (Appendix S1: Figures S1–S3). Species (rows) and stations (columns) were hierarchically clustered to highlight compositional structure, with colour intensity indicating relative abundance.

2.4 | Trait-Based Analyses

In order to investigate trait distributions, eight categorical traits were selected based on their affiliation to either resource strategies or dispersal abilities (Table 1). To ensure consistency

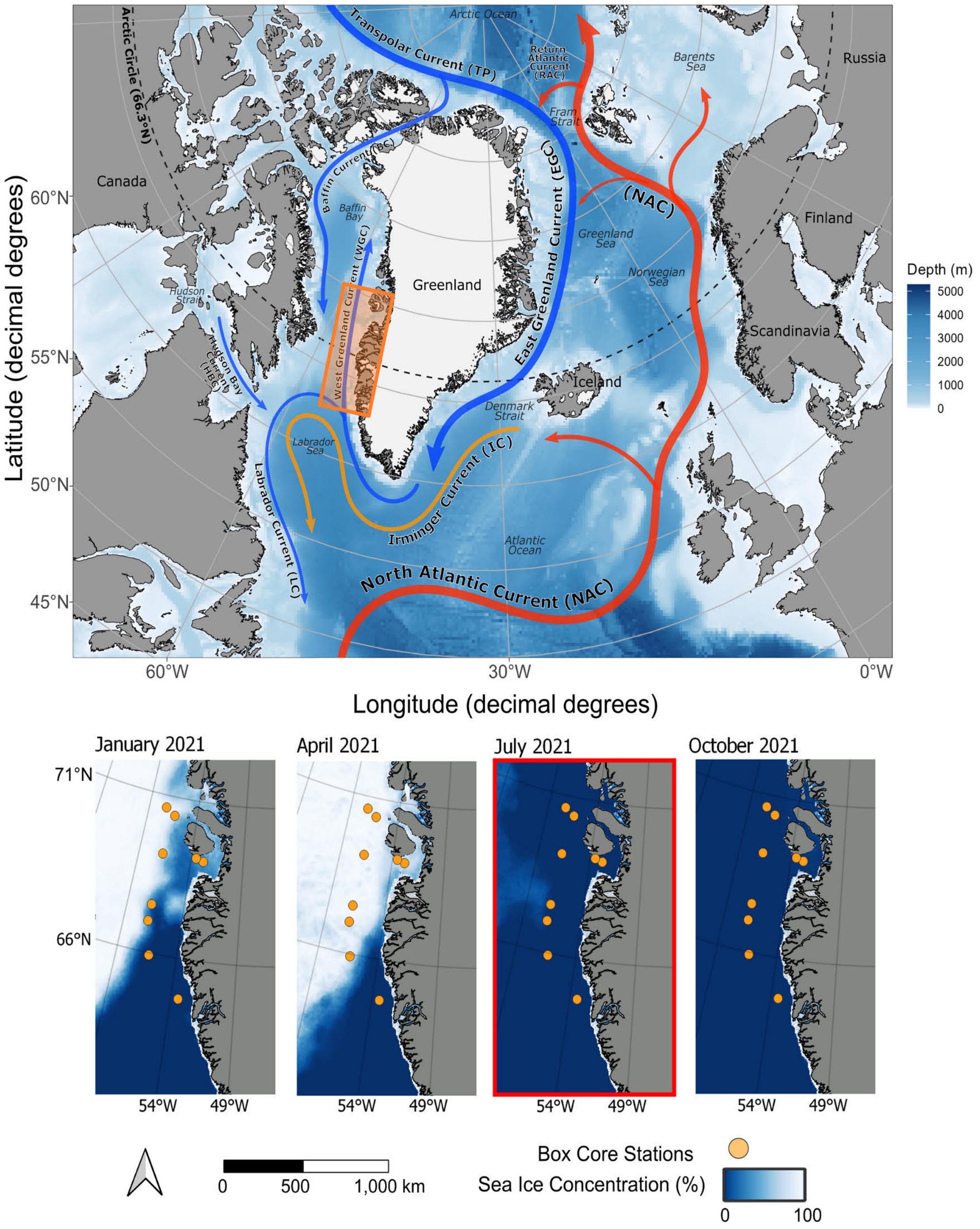

FIGURE 1 | Top panel: West Greenland map showing the study area, benthic sampling stations during the R/V Dana Cruise, 2021 (orange box), and the surrounding ocean currents. Bottom panels: The sea ice concentration is presented across the year to show its annual variability and North–South gradient. Sea ice data from Copernicus Marine Service (Arctic Ocean Sea Ice Analysis and Forecast) and the maps are made in QGIS, Greenland. The red box indicates the month in which data collection took place.

across Arctic trait-centric research, trait data were sourced from the Arctic Trait Database (https://www.univie.ac.at/arctic traits/, Accessed: January 2025). In instances where traits were absent from the Arctic Trait Database at the most refined taxonomic level, an extensive review of the literature was undertaken to maintain the highest possible taxonomic resolution, or alternatively, the trait was assigned a score of zero to avoid introducing bias into the results. While this approach represents a conservative assumption, treating unknown affinities as absence rather than missing information, we favoured preserving a consistent trait structure across taxa given the high overall trait coverage of the dataset (82%–100% completeness for all but one trait category; tolerance traits 68%; Tables S1 and S2). The fuzzy coding method was employed to accommodate the capacity of taxa to exhibit various categories within a trait. Consequently, taxa were allocated one or multiple categories according to their degree of affinity, utilising a scoring system ranging from 0 to 3, where 0 indicates no affinity and 3 signifies a strong affinity towards a category (Chevene et al. 1994b). Taxa demonstrating equal affinity for multiple categories within a biological trait received the same score for those categories. Raw trait plots of each biogeographic group over latitude are in the Figure S4.

2.5 | Environmental Variables

Latitude, longitude, water depth (m), salinity, potential temperature (θ°C), and oxygen ($\mathrm{mL\,L^{-1}}$) were extracted from the SBE 911plus CTD sampling on board R/V Dana, launched 2 m above the seafloor, and processed using Ocean Data View (version ODV 5.7.2). The distance (km) between stations was calculated by converting the coordinates using the R package "geosphere" (Hijmans et al. 2024). Sea ice concentration data for 2021 were downloaded from the European Copernicus Marine Service Information (Arctic Ocean—Sea Ice Concentration Charts—Svalbard and Greenland, 2024; https://doi.org/10.48670/moi-00128). The minimum, mean, and maximum data were extracted and the mean sea ice concentration plotted in QGreenland (QGIS; Moon et al. 2024) (Figure 1). As currents play an important role in species distribution in the West Greenland Shelf area, bottom water current speed (m/s) data were extracted for each station from Copernicus Marine Service Information (Global Ocean Physics Analysis and Forecast, 2024; https://doi.org/10.48670/moi-00016) as July monthly averaged sea water velocity in 2022 since this data were not available for 2021.

In addition, two sediment cores (~15 $\mathrm{cm^2}$) were taken from each box core replicate for organic content and sediment grain size analyses. Organic content was measured by means of the Loss of Ignition (LOI) method (see Appendix S2 for protocol), while exact values for Carbon and Nitrogen content were measured using the C/N-Analyser; Europa Scientific ANCA-MS 20-20 15N/13C mass spectrometer. Sediment grain size analysis processing included calculating water content, organic content (via oxidation using hydrogen peroxide), followed by the SediGraph technique, which allows for the calculation of composition into cumulative fractions (%) of mud, silt, sand, and gravel (for full methods, see Appendix S3).

2.6 | Data Analysis

To characterise patterns in benthic community structure across the West Greenland shelf, we applied complementary taxonomic and functional diversity frameworks. Taxonomic metrics describe changes in species identity and abundance, whereas functional metrics capture shifts in the distribution of biological traits that contribute to ecosystem processing. Together, these approaches allow us to distinguish whether spatial differences in community composition arise from species turnover or nested gradients, and whether communities are structured by similar or contrasting trait strategies across the north–south gradient.

2.6.1 | Taxonomic Diversity Metrics

Taxonomic α diversity was quantified at each station to characterise local variation in species number and evenness across the West Greenland shelf, using species richness, which counts the number of species within a community, and species diversity measured by the Shannon diversity index (H′) (Equation S1), where higher values indicate communities with greater species richness and evenness.

β-diversity of species composition between stations was quantified to elucidate spatial variation in benthic community composition across the West Greenland shelf, including differences among Arctic, Boreal, and Cosmopolitan species assemblages (Baselga 2009). Total β-diversity was calculated by using species abundance data and the Ružička dissimilarity index (Equation S2) (Ružička 1958; Legendre and De Cáceres 2013; Legendre 2014), which captures the overall dissimilarity between stations. Unlike presence–absence indices, the Ružička index incorporates shared species abundances and is therefore well suited to benthic communities characterised by uneven species distributions. Compared with Bray–Curtis, which follows the Sørensen index and is more sensitive to large differences in species abundances, the Ružička index is an extension of the Jaccard index and is less influenced by differences in total community abundance. Furthermore, the Ružička dissimilarity index clearly decomposes total β-diversity into per-species components of turnover (known as balanced variation in abundance) or nestedness (known as abundance difference or abundance gradients), which facilitates interpretation of the species contributing most strongly to spatial changes in biodiversity (Baselga 2013; Legendre 2014). For full derivations, see Equations S2 and S3.

2.6.2 | Functional Diversity and Trait Composition

Functional diversity was assessed to quantify how trait composition varies among stations and biogeographic groups. We calculated functional richness (FRic), functional diversity (Rao's quadratic entropy, RaoQ), community-weighted means (CWMs), and functional β diversity to evaluate whether communities differ primarily in the range of traits expressed, the dominance of particular trait strategies, or the spatial reordering of similar functional roles.

Functional richness (FRic) is the complement to species richness and is calculated as the volume of functional trait space occupied by the community, based on convex hulls calculated from a PCoA of trait distances. The results were standardised (0–1), enabling meaningful comparisons across biogeographic groups. Functional diversity was assessed using Rao's quadratic entropy (RaoQ; Rao 1984; Botta-Dukát 2005), which extends the Shannon diversity framework by incorporating species' trait differences together with their relative abundances. It is computed via the *FD* package (Laliberté et al. 2025), based on a Gower distance matrix derived from standardised trait data, as the sum of pairwise functional distances between species, weighted by the product of their relative abundances. To examine spatial variation in dominant trait expression, we calculated community-weighted means (CWMs) for each trait category. CWMs represent the abundance-weighted average trait composition of a community and reflect which traits are most strongly expressed at the community level, rather than the species level. CWMs were also calculated using the FD package in R, based on standardised species abundance data and fuzzy-coded trait affinities. Functional β diversity was assessed using the BAT package (Cardoso et al. 2025) in R, which allows decomposition of functional dissimilarity into turnover and nestedness components analogous to the taxonomic framework, while supporting rarefaction and the simultaneous analysis of multiple stations. This approach quantifies whether spatial differences among stations reflect replacement of functional trait combinations or reordering of similar trait assemblages across space.

For visualisation, we reported each biogeographic group and component, the five highest-contributing species or traits and displayed their species site-wise abundances or trait CWMs as heatmaps. All the diversity analyses were run on the total community and on each individual biogeographic group of species using R Software (version 2024.09.1; packages "vegan" (Oksanen et al. 2025), "FD" (Laliberté et al. 2025), "adespatial" (Dray et al. 2025), "BAT" (Cardoso et al. 2025), and "betapart" (Baselga et al. 2025)).

2.6.3 | Environmental Analyses

Prior to environmental distance modelling, we first assessed correlations among variables related to water mass properties, sediment characteristics and spatial gradients, which revealed substantial collinearity among environmental variables (Figure S5). To retain important environmental information rather than drop variables, we performed principal component analyses (PCA) on each subset of variables. For water properties (depth, salinity, temperature, oxygen, and current speed) and sediment characteristics (fractions of substrate (sand, mud, silt, and gravel), and carbon and nitrogen content), the first three axes were retained, and two were retained for spatial gradients (latitude, longitude, sea ice, and distance). The PC axes were selected using scree plots (Figure S6) and by retaining axes that accounted for ~98% of the variation. The sediment, water and spatial PC axes were then used in subsequent analyses in place of the original variables.

To identify the environmental gradients most strongly associated with patterns in species and trait distributions, we used a Multiple Regression on distance Matrices (MRM) framework. This approach models pairwise ecological dissimilarity as a function of environmental dissimilarity, therefore capturing the effects of multivariate environmental gradients on community composition and trait structure. Thus, it complements the β-diversity approach, which also uses dissimilarity matrices and accounts for highly variable environmental gradients found across our study sites. To identify the optimal set of environmental predictors (i.e., the best composite gradient) for each community response, we implemented an automated model selection routine. For each species or trait-based dissimilarity matrix (Bray–Curtis distances on species and Euclidean distances for traits), we iteratively evaluated all combinations of 1 to k predictor variables (up to a maximum of eight). For each combination, we calculated a scaled Euclidean environmental distance matrix and fit an MRM model ($n = 999$ permutations) using the ecodist package (Goslee and Urban 2023) in R software. The best model was selected based on the highest R^2 value and lowest permutation p-value. This procedure was applied across the full dataset as well as separately for each biogeographic group (Arctic, Boreal, and Cosmopolitan).

We further disentangled the independent environmental contributions by re-running MRM models using only the individual variables from the best-performing composite model. This allowed us to estimate the magnitude and direction (β-coefficient) as well as the significance of each variable's effect on species composition, trait community-weighted means (CWMs), and multiple β-diversity components (total, turnover, and nestedness). These models were conducted separately for each biogeographic group, enabling direct comparisons of environmental filtering across assemblages. This distance-based modelling approach was integrated with our trait-based framework to explore how environmental gradients shape dispersal and resource strategies. By linking environmental predictors to shifts in trait composition and β-diversity, we evaluated how mixing among these functional groups may alter ecological dynamics under ongoing climate-driven changes in the Arctic marine system.

3 | Results

3.1 | Spatial Distribution and Biogeography

By combining species occurrence and trait data, we show a heterogeneous distribution of benthic infaunal communities along the West Greenland shelf. Contrary to our expectation, the relative contributions of Arctic, Boreal, and Cosmopolitan taxa did not exhibit a consistent latitudinal shift; rather, all three groups occurred across the full shelf gradient (Figure 2).

Taxonomic composition (e.g., phyla) was variable across stations, with no consistent spatial trend (Figure 2B). Boreal species made the largest number of taxa (68), followed by Cosmopolitan (53) and Arctic (40). The dominant phyla overall were annelids (mostly polychaetes), molluscs (mostly bivalves), and arthropods (largely malacostracans), although annelids and molluscs accounted for the majority of individuals. Among Arctic species, molluscs were especially abundant, particularly at stations 2, 3, 5, 7, and 9. Cosmopolitan species exhibited a mixed taxonomic composition across stations, with no single dominant group; although annelids and molluscs were frequently present.

In terms of species richness, taxa at most stations were relatively balanced (~1/3) among Arctic, Boreal, and Cosmopolitan groups, with the exception of stations 5 and 9 (Arctic-dominated) and station 6 (Boreal-dominated) (Figure 2C). Notably, stations 5 and 6 were located adjacent to the glacier in Disko Bay and had the lowest overall species richness across the dataset. Station 4 contained the highest proportion of Cosmopolitan taxa (43%),

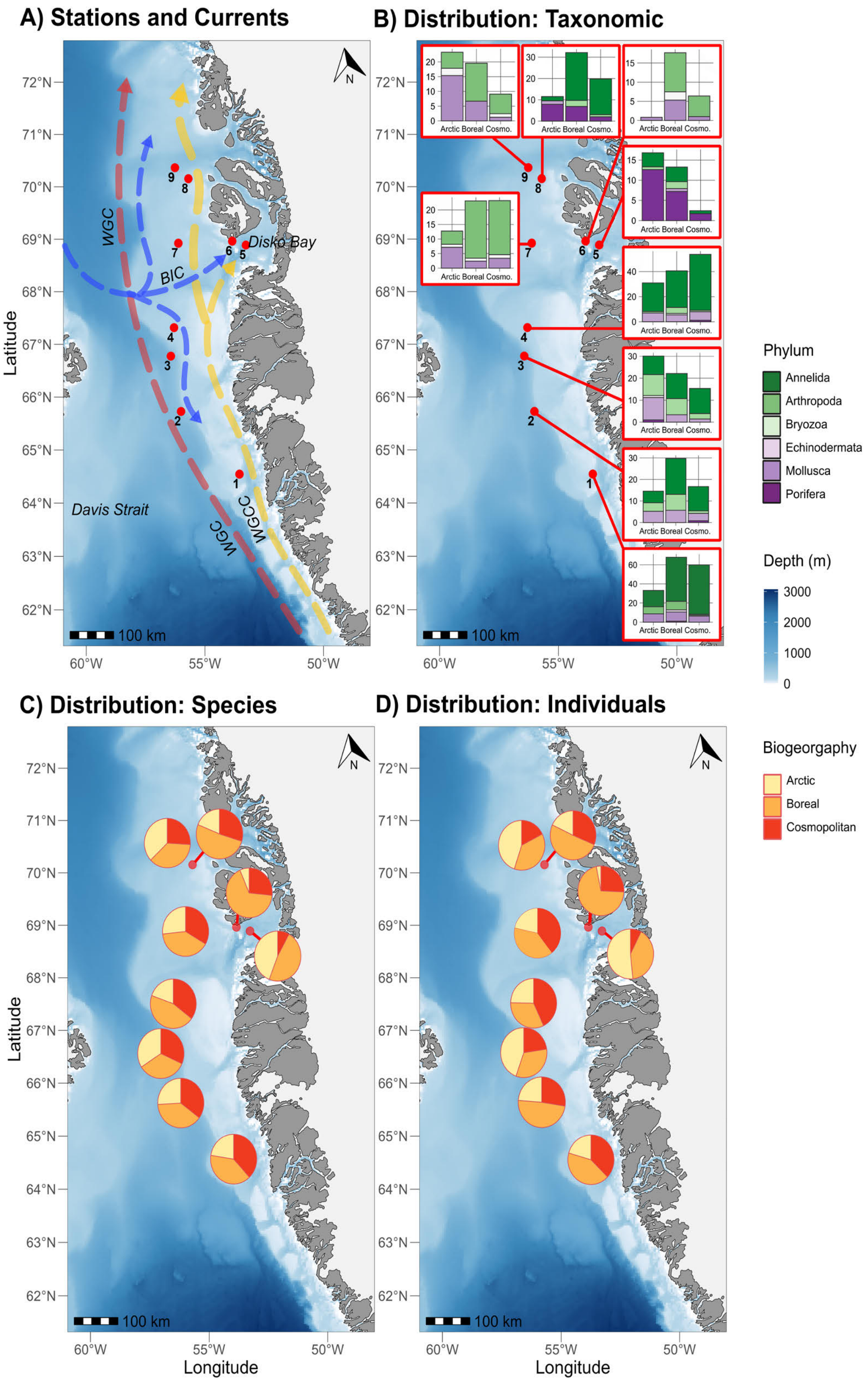

FIGURE 2 | Legend on next page.

FIGURE 2 | The study area and community structure across nine stations shown as (A) Stations, bathymetry, and principal currents (WGC—West Greenland Current; WGCC—West Greenland Coastal Current; BIC—Baffin Island Current); (B) abundances by phylum (stacked bars); *y* axis is individuals per m^2, and the *y*-axis scale varies among stations; (C) species richness by biogeographic group (Arctic, Boreal, Cosmopolitan); (D) abundance of individuals by biogeographic group (Arctic, Boreal, Cosmopolitan).

TABLE 1 | Summary of selected benthic traits and their categorical modalities[a].

Trait	Definition	Category
Larval Development	Mechanism of larval development, including types such as pelagic/planktotrophic (LD1), pelagic/lecithotrophic (LD2), and benthic/direct development (LD3)	Dispersion
Mobility	Degree of movement capability of the organism: none (MO1), low (MO2), medium (MO3), and high mobility (MO4)	Dispersion
Adult Movement	Type of movement exhibited by adults, including sessile (MV1), burrower (MV2), crawler (MV3), and swimmer (MV4)	Dispersion
Reproduction	Reproductive strategy, such as asexual reproduction (R1), sexual reproduction with external fertilisation (R2), internal fertilisation (R3), or brooding (R4)	Dispersion
Size	Body size categories of organisms: small (S1), small-medium (S2), medium (S3), medium-large (S4) and large (S5)	Resource Strategies
Living Habit	Habitual living mode, including free-living (LH1), crevice dwelling (LH2), tube dwelling (LH3), burrowing (LH4), epizoic (LH5), or attached lifestyles (LH6)	Resource Strategies
Feeding Habit	Feeding strategy, such as deposit feeding (FH1), filter/suspension feeding (FH2), opportunist/scavenger (FH3), predator (FH4), or parasite/commensal/symbiotic (FH5)	Resource Strategies
Tolerance	Tolerance (low (T1), medium (T2) and high (T3)) to environmental factors, including salinity, temperature, hypoxia, pollutants, and other stressors	Resource Strategies

[a] Trait data were compiled primarily from the Arctic Traits Database (Degen & Faulwetter, 2019) and supplemented with Armitage et al. (2025) and references therein.

though Boreal and Arctic species were also well represented (Figure 2C).

When considering abundances rather than richness, patterns followed that of species richness but still without a consistent spatial trend (Figure 2D). While communities were still relatively mixed, four stations (1, 2, 6, 8) had a higher proportion of individuals of Boreal species, while three stations (3, 5, 9) had more individuals of Arctic species. Cosmopolitan species dominated at station 4 and were approximately equal to Boreal species at station 7. Thus, although species richness was often relatively balanced across groups, abundances revealed stronger contrasts in dominance among biogeographic categories.

3.2 | Trait-Based Comparisons and Diversity

The three biogeographic groups show more similarities than dissimilarities in the traits they express, initially suggesting little difference when analysing them separately rather than altogether. When comparing the average species affinity for each category of trait (Table S3), there were similar traits being expressed in terms of the highest affinity and the lowest affinity to trait categories, regardless of biogeographic affinity. The strongest affinities are for low mobility, small-medium size, and deposit feeding, and almost no affinity for high mobility, large body size, and parasitic/symbiotic feeding habits. Therefore, in this case, looking at the average species affinity to traits across the total community gives a good indication of the trait composition and can suggest that each biogeographic grouping does not express notably different traits from one another at this level of categorical trait information.

The same dominant traits were also evident when examining the community-level trait communities (CWMs) (Figure 3), but the variability in the non-dominant trait categories is much more clearly identifiable when comparing the biogeographic groupings. The most notable differences can be seen in the Arctic group, which differs in the most dominant trait versus other groups (Boreal and Cosmopolitan); in size (small vs. small-medium), living habit (burrowing vs. tube dwelling), tolerance (high vs. more variability), and larvae development (benthic/direct vs. pelagic/planktotrophic) (Figure 3). Therefore, the species in this area can be characterised by having low mobility and burrowing behaviour, having external sexual reproduction, and either benthic direct development (Arctic species) or planktotrophic larvae (Boreal and Cosmopolitan), with some variation for lecithotrophic larvae.

3.3 | Taxonomic and Functional Diversity Indices

Taxonomic α-diversity measures (species richness and Shannon diversity) were marginally higher in the Boreal group compared to the Arctic and Cosmopolitan groups, yet both metrics declined significantly with increasing latitude

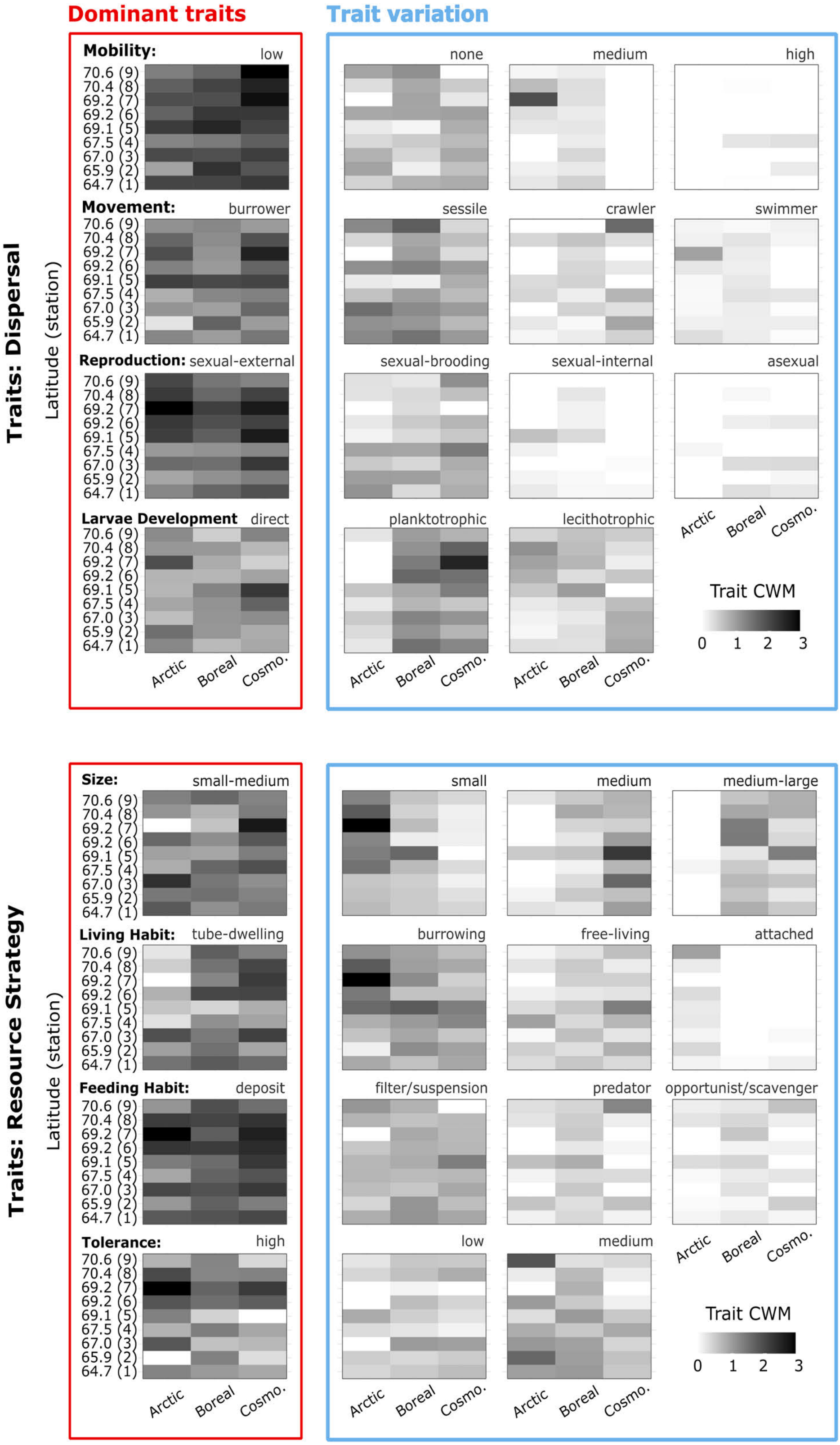

FIGURE 3 | Legend on next page.

FIGURE 3 | Community-weighted trait means (CWM; see legend for colour key) of benthic infaunal traits at each station in West Greenland, expressed by latitude. The red box highlights those that are most dominantly expressed at the community level, while the blue box highlights where there is greater variation between groups. Note that the Arctic group does not always share the same dominant trait category as the other groups (e.g., living habit, movement, and size).

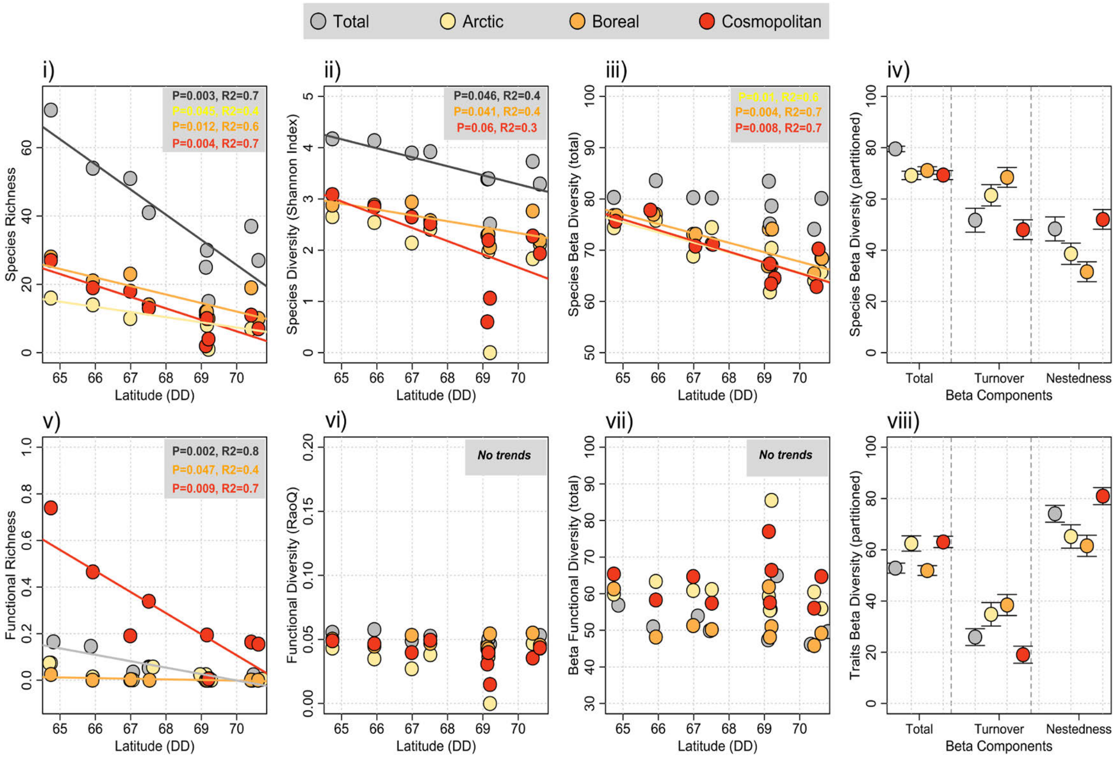

FIGURE 4 | Diversity measures (i–iv taxonomic, v–viii—functional) in the whole benthic community and biogeographical groups are shown against latitude. Only significant linear models are shown with the associated trendline and reported text. Colours represent biogeographical groups (see legend).

across the total community and within all three biogeographic groups (Figure 4i,ii), indicating a latitudinal loss of taxonomic diversity. Species β-diversity was consistently high across all stations (mean ± SD: 79.5 ± 3.2), revealing distinct assemblages between stations (Figure 4iii). This pattern was consistent within each biogeographic group. Partitioning of species β-diversity showed that turnover dominated in the Boreal group (mean ± SD: 68.4% ± 11.6%), was slightly lower in the Arctic group (61.4% ± 12.5%), and was nearly evenly split between turnover and nestedness in the Cosmopolitan group (turnover: 48.0% ± 11.6%, nestedness: 52.0% ± 11.6%) (Figure 4iv).

Functional richness was low overall (range: 0.1–0.4) and declined significantly with increasing latitude in Cosmopolitan species (Figure 4v). In contrast, the Arctic and Boreal groups showed very low functional richness (< 0.2) across all stations, with a declining trend northward. When species abundances were considered, functional diversity (RaoQ) remained consistently low across all groups (mean ± SD: 0.04 ± 0.008), with no clear spatial trends (Figure 4vi). Functional β-diversity was moderately high (mean ± SD: 52.8 ± 6.0) and did not vary with latitude (Figure 4vii) but was predominantly driven by nestedness rather than turnover in all groups (Figure 4viii), indicating that high species turnover among stations did not translate into diversification of trait strategies. This pattern aligns with the dominance of shared traits across sites (Figure 3), indicating functional redundancy and constrained trait space despite high taxonomic turnover.

The species contributing the most to β-turnover (balanced variation) and β-nestedness (abundance difference) in the total community (grey panels) were not from a single biogeographic subset but instead included taxa from all biogeographic groups (Figure 5A,B). Thus, the overall community reflects an integration of Arctic, Boreal, and Cosmopolitan assemblages, rather than dominance of local (turnover) or widespread (nestedness) species by any single subset. Yet across groups, the species contributing most were taxonomically concentrated in just two phyla, molluscs (bivalves) and annelids (polychaetes), indicating the role of a relatively narrow set of lineages in driving spatial dissimilarity.

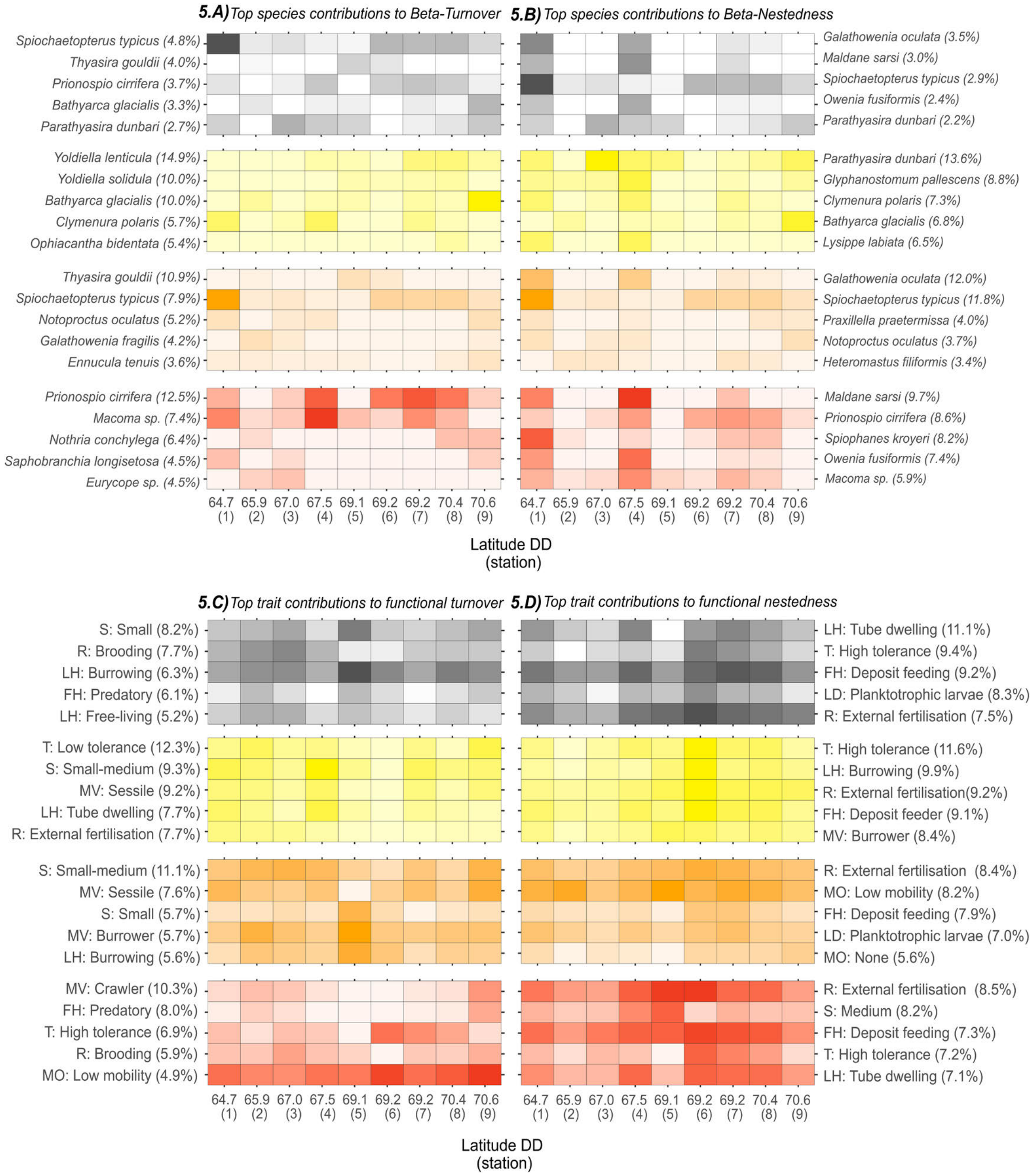

FIGURE 5 | The top five species (A, B) and traits (C, D) of each biogeographic group (grey: The total community, yellow: Arctic, orange: Boreal, red: Cosmopolitan), which represent the highest contributions to turnover (balanced variation; A, C), and nestedness (abundance difference; B, D) among stations, are shown via their abundance or community weighted means (CWM). The richer the colour, the higher the abundance or CWM at the station (*x*-axis). The percentages in the brackets represent how much the species (traits) contribute to either β-diversity component.

Examining contributions within each biogeographic group revealed stronger species-specific signals than in the total community. This is consistent with the observation that the top contributors in the total community each accounted for no more than 5% of turnover or nestedness (Figure 5A,B, respectively), whereas in the separate biogeographic groups, the strongest contributors reached up to 13%. Partitioning by biogeographic affinity therefore highlights which species within each group exert greater influence: in the Arctic group, just five species explained 45% of turnover and 43% of nestedness, despite the group's relatively smaller species pool. In Boreal and Cosmopolitan groups, the top five species also accounted for substantial fractions of dissimilarity (turnover: 31.8% and 35.3%; nestedness: 34.9% and 39.8%, respectively).

Patterns of trait contributions revealed group-specific contrasts. For example, the top contributors to total community functional turnover (balanced variation; Figure 5C) were small body size

TABLE 2 | Summary of principal component analyses (PCA) on water, sediment and spatial environmental variables. For each PCA axis, the percentage of variance explained, main loadings (positive or negative associations), and the corresponding environmental gradient interpretation are shown.

	Principal component	Variance explained (%)	Main loadings (±)	Environmental gradient interpretation
Water variables	PC1	49	Depth (+), Salinity (+), Oxygen (−)	Deep, high-salinity, low-oxygen versus shallow, low-salinity, high-oxygen environments
	PC2	29	Temperature (+), Oxygen (+)	Warm, oxygen-rich versus cold, oxygen-poor environments
	PC3	20	Current speed (−)	Low versus high current velocity
Total variance		98		
Sediment variables	PC1	62	Sand (−), Mud (+), Carbon (+), Nitrogen (+)	Fine, organic-rich versus coarse, sand-dominated sediments
	PC2	22	Silt (−), Sand (+)	Low silt versus high silt content
	PC3	14	Gravel (−)	High gravel versus low gravel content
Total variance		98		
Spatial variables	PC1	73	Sea Ice (+), Latitude (+), Distance (+), Longitude (−)	Spatial gradient from west (low latitude, low sea ice concentration) to northeast (high latitude, high sea ice concentration)
	PC2	25	Longitude (+), Latitude (+), Sea ice (−)	East–west spatial structure and sea ice influence
Total variance		98		

and brooding, whereas Arctic assemblages had low tolerance and sessile or tube-dwelling forms. Boreal turnover was linked to size classes and burrowing, while Cosmopolitan assemblages were distinguished by crawler mobility, high tolerance, and predation; traits often associated with higher trophic levels or disturbance-tolerant strategies. Nestedness at the trait level (Figure 5D) was more consistent across groups. External fertilisation, deposit feeding, and high environmental tolerance were among the leading contributors in Arctic and Cosmopolitan subsets, and also in the total community. Notably, station 6 (69.2° N) showed simultaneous peaks in several high-contributing traits, suggesting local dominance of a limited set of viable traits shaped by environmental filtering. Together, these top contributing traits still mirror the dominant trait profiles outlined in earlier analyses.

3.4 | Environmental Predictors of Species and Trait-Based Community Structure

Principal component analyses revealed distinct environmental gradients for water, sediment, and spatial variables (Table 2). For water properties, the first three principal components explained 98% of the total variance, with PC1 primarily reflecting a depth–salinity gradient opposed to oxygen, PC2 capturing a temperature–oxygen contrast, and PC3 associated with current speed. For sediment characteristics, three components accounted for 98% of the variance, separating fine, organic-rich sediments from coarser substrates and distinguishing variation in gravel content. Spatial variables were summarised by two principal components explaining 98% of the variance, representing a west–east gradient associated with latitude and sea ice concentration, and a secondary longitudinal structure. These PC axes were used as environmental predictors in subsequent analyses.

Using Multiple Regression on distance Matrices (MRM) and the results from the PCA analyses, we found that joint gradients of sediment characteristics, water column structure, and spatial–climatic gradients were consistently significant predictors of benthic community variation, rather than single drivers (Figure 6). Composite environmental distance matrices built from optimal combinations of PCA-derived gradients explained a substantial proportion of variance in community dissimilarity ($R^2 = 0.24$–0.61; $p < 0.01$ in most models; Table S4). Species β-diversity, functional β-diversity, and trait community-weighted means (CWMs) all showed strong associations with these multivariate gradients, particularly in biogeography-specific models (Figure 6). For example, functional β-diversity of Cosmopolitan species was strongly associated with sediment PC1, water PC1, and spatial PC2 ($R^2 = 0.54$, $p = 0.002$), while trait CWMs (dispersal and resource traits) for all taxa were best explained by a combination of sediment PC1 and spatial PC2 ($R^2 = 0.43$–0.46, $p < 0.005$). Nestedness components of β-diversity for Arctic and Cosmopolitan assemblages were also well explained by composite environmental distance matrices dominated by sediment PC2 and spatial PC2 ($R^2 = 0.28$–0.39, $p < 0.01$). These associations reflect environmentally mediated structure, rather than a simple latitudinal gradient.

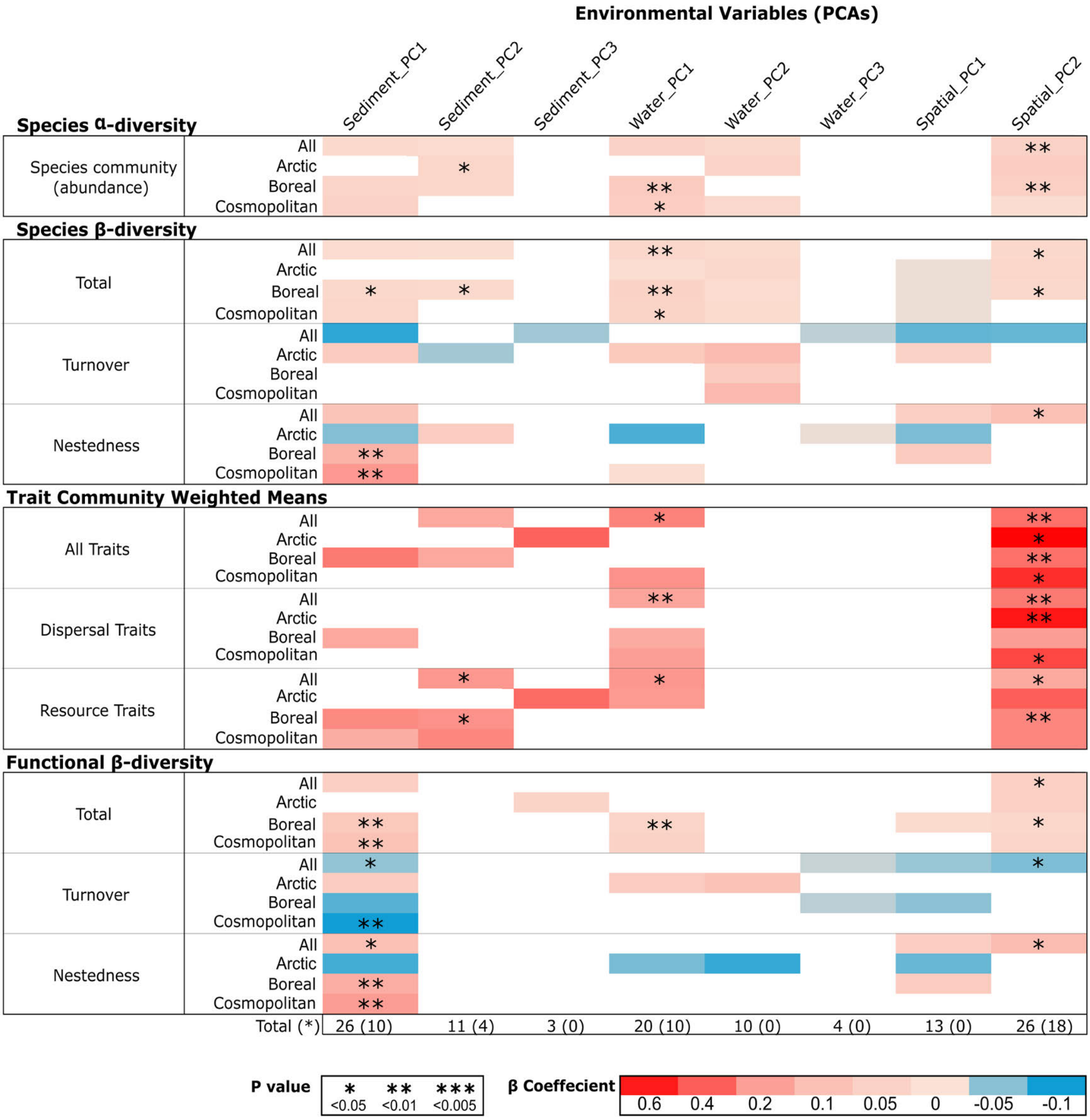

FIGURE 6 | Synthesised results from two Multiple Regression on distance Matrices (MRM) approaches. Coloured cells indicate environmental variables selected in the best-fitting multivariate (composite) environmental dissimilarity models for each response variable (rows). Overlaid β-coefficients and asterisks on the heatmap denote the strength and significance of each variable (see legend). Full model statistics for both the composite and individual MRMs are provided in Table S4.

To disentangle the relative contribution of each selected variable, individual MRM models were fit using predictors from the best composite sets. This approach revealed significant effects across sediment, water, and spatial variables, but with varying effect sizes depending on the response and biogeographic group (Figures 6 and 7). Sediment PC1 (representing an organic-rich and higher fractions of mud) and sediment PC2 (silt content) were particularly influential, significantly predicting variation in species β-diversity (Boreal, $\beta = 0.235$, $p = 0.036$), functional β-diversity (Cosmopolitan, $\beta = 0.329$, $p = 0.003$), and trait CWMs (All taxa, $\beta = 0.428$, $p = 0.007$) (Figures 6 and 7). Water PC1, capturing a depth-salinity-oxygen axis, was also a frequent driver, significantly associated with CWMs (All and Cosmopolitan; $p < 0.01$) and total functional β-diversity (Cosmopolitan; $\beta = 0.316$, $p = 0.013$) (Figures 6 and 7). Spatial PC2, representing a longitudinal and latitudinal ice-structured gradient, emerged as a key predictor across many trait-based models and β-diversity responses, particularly for Cosmopolitan taxa (Figure 7).

When CWMs were disaggregated into resource-use traits and dispersal traits, distinct patterns emerged. Dispersal CWMs were most strongly associated with spatial PC2 and sediment PC1, especially for Arctic and Cosmopolitan taxa, suggesting that geographic structure and substrate type shape the distribution of dispersion-related traits. In contrast, resource-use CWMs were more sensitive to sediment PC2 and water PC1, indicating

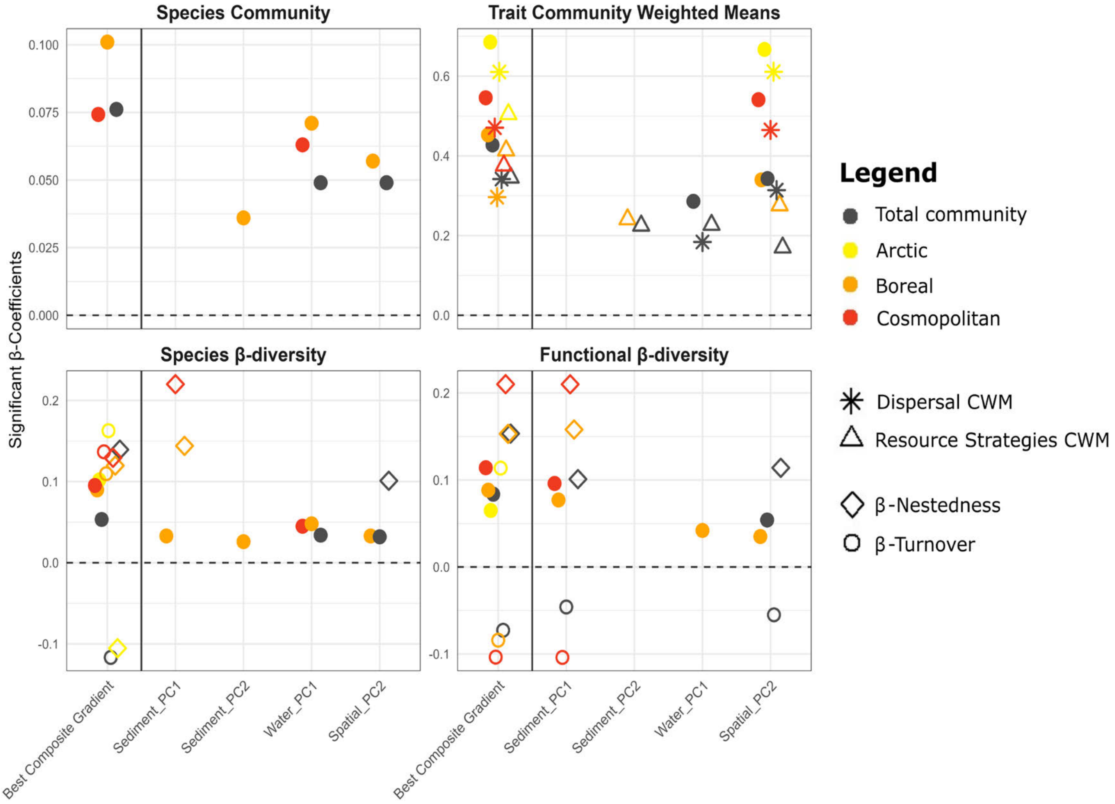

FIGURE 7 | Significant β-coefficients from Multiple Regression on distance Matrices (MRM) models showing the effects of environmental predictors on species and trait-based community structure (see Figure 6 for model structure and Table S4 for R^2 values). Each panel represents a response category. Filled circles correspond to community-level or total β-diversity metrics, while open symbols indicate β-diversity components (turnover or nestedness) and resource or dispersal trait CWMs. Horizontal dashed lines denote model intercepts (β = 0).

a greater influence by local sediment characteristics and hydrographic structure. These patterns were broadly consistent with those observed in the total CWMs but highlighted additional trait-specific environmental filters that are masked when using aggregate trait summaries alone.

4 | Discussion

Here we identify the spatial distribution of benthic infaunal invertebrates in relation to biogeographical classifications, to gain a better understanding of biodiversity and ecosystem patterns along a north–south gradient on the West Greenland shelf. Our main finding shows that, although the study region is geographically Arctic, the benthic assemblage is biogeographically mixed, with Arctic, Boreal, and Cosmopolitan species each contributing approximately one-third along the gradient from Nuuk to Disko Bay. This outcome partially contradicts our first hypothesis, which predicted a clear latitudinal gradient, and raises questions about the historical and ecological processes that have shaped this distribution. The shelf supports a diverse benthic assemblage (161 taxa), characterised by a high Shannon index and elevated species β-diversity, largely driven by turnover, with molluscs, annelids, and arthropods being the dominant groups. However, trait-based analyses reveal low functional diversity and a highly nested trait structure across the gradient, highlighting trait convergence despite high species diversity. These results reject our second hypothesis, demonstrating that high taxonomic turnover along the shelf is decoupled from functional turnover and instead reflects strong trait convergence. This consistent trait dominance, despite high species diversity and turnover, helps to refine our third hypothesis. Rather than discrete environmental gradients acting independently, interacting sedimentary, hydrographic, and spatial–climatic gradients act as strong environmental filters, jointly constraining viable trait strategies and reinforcing functional convergence across the shelf.

There were three additional observations outside of the main findings: First, the Boreal group exhibited greater trait variability but still conformed to dominant trait profiles, and its functional richness and diversity remained consistently low despite higher species richness and abundance. Second, clear trait differences between Arctic and Cosmopolitan species, in living habit (burrowing vs. tube-dwelling), body size (small vs. small-medium), and larval development (benthic direct vs. planktotrophic larvae), suggest niche partitioning or potential ecological competition. Third, spatial shifts in species abundance and community-weighted trait means were more or less prominent at particular stations, as revealed through β-diversity contributions of nestedness and turnover. Given the ecological importance of the main findings and the observations, we discuss each in greater detail in the following section. Collectively, they underscore the role of strong environmental filtering in community assembly, possibly intensified by ongoing climate change, shaping a functionally constrained yet taxonomically diverse benthic community with ecological and conservation implications.

4.1 | Main Findings

The finding that Arctic, Boreal, and Cosmopolitan species each contribute approximately one-third to the benthic community across the north–south gradient points to a mixed biogeographic structure that complicates a simple Arctic classification of the region. Furthermore, the species contributing most to both β-turnover and β-nestedness were distributed across all three biogeographic groups, further highlighting that community assembly is shaped by shared environmental tolerances rather than strict latitudinal boundaries. In a transitional region such as this (where Arctic and sub-Arctic influences converge), the observed composition and diversity patterns raise the question of whether this is a historically stable mixing zone or if there is an ongoing redistribution of species in response to environmental change. Comparisons with Svalbard fjords (Włodarska-Kowalczuk et al. 2004) and the Northeast Greenland shelf area (Armitage et al. 2025) support the dominance of Boreo-Arctic benthic assemblages. Additionally, earlier zoogeographic work from Disko Bay (Schmid and Piepenburg 1993) found that ~70%–80% of species were classified as Boreo-Arctic, 10% as strictly Arctic, and 6%–14% as Cosmopolitan. Although our classification separates Arctic and Boreal species rather than grouping them into a Boreo-Arctic category, both datasets highlight that the fauna is dominated by Arctic/Boreal overlap, with Cosmopolitan species forming a smaller but consistent fraction of the community. The somewhat higher fraction of Cosmopolitan species in our data may reflect broader shelf coverage and recent biogeographic shifts, or could be an artefact of our classification approach or methodological choices, including differences in sampling methods (e.g., sieve mesh size or coring vs. trawl-based sampling), underscoring how methodological differences and the estimation of species' biogeographic contributions can shift depending on spatial, temporal, and taxonomic resolution. Together, these findings suggest that Eurasian Arctic shelves are already structured by mixed assemblages, with overlap driven by both evolutionary history and present-day connectivity. Whether this reflects a long-standing equilibrium or signals reorganisation remains unresolved and will require temporal data and broader spatial comparisons across Arctic–sub-Arctic transition zones.

To better understand the present-day structuring processes, we applied environmental models to explain patterns of species and trait composition. Our MRM results identify three principal gradients: sediment composition (PC1: ranging from fine, organic-rich muds to coarser sands; PC2: silt content), hydrographic structure (PC1: water depth, salinity, oxygen), and a spatial axis (PC2: latitude, sea-ice cover, and longitude), which together explain 24%–61% of community dissimilarity. Sediment loadings PC1 and PC2 were among the most frequent and influential predictors of community composition and functional structure, reflecting local habitat suitability and resource availability for infauna. However, nestedness in both Arctic and Cosmopolitan assemblages was explained by differences in sediment PC2 and spatial PC2 ($R^2 = 0.28$–0.39), reflecting gradients with broader temporal and geographic scales. This may be especially relevant for Arctic taxa, whose dispersal-limiting traits, such as benthic or direct development, could make them more sensitive to long-standing habitat constraints. Notably, outside of the nestedness species model, Arctic species generally showed weaker model fits, likely due to patchy distributions and low detectability, which reduce statistical power even when local associations exist.

Notably, bottom current speed (water PC3) did not emerge as an important predictor of species or trait composition in our models, despite previous work in the same West Greenland region reporting stronger currents in southern areas relative to northern sites (Gougeon et al. 2017). Mean bottom current speeds were low across stations (mean $\approx 0.05\,\mathrm{m\,s^{-1}}$, range ≈ 0.01–$0.11\,\mathrm{m\,s^{-1}}$), and so it is likely the spatial resolution of the current data ($0.083° \times 0.083°$, ~5 km), rather than the one-year mismatch between sampling and bottom current datasets, limited current-related effects. Consequently, these data should be interpreted as regional-scale estimates of circulation and may not have captured fine-scale hydrodynamic variability associated with complex bathymetry, such as localised acceleration or up- and downwelling around sills and troughs, which are likely to influence dispersal and biogeochemical fluxes in Arctic benthic systems (Holtappels et al. 2013; Gougeon et al. 2017; Meyer et al. 2017).

Our trait-based analyses reveal that Arctic, Boreal, and Cosmopolitan species are dominated by a single leading modality within each trait category; specifically, deposit feeding among feeding types, low mobility among mobility traits, and small-to-medium size among body size classes, while more energetically costly strategies such as predation, scavenging, and high mobility are rare or absent. Schmid and Piepenburg (1993) likewise highlighted the prevalence of deposit feeders in Disko Bay, particularly among polychaetes and bivalves, reinforcing that benthic functioning in high-latitude shelves is consistently shaped by a narrow set of feeding strategies well adapted to organic-rich, sedimentary environments. Building on this prior context, our results show that trait structure is associated with a small number of multivariate environmental gradients rather than sediment characteristics alone. For example, both Cosmopolitan taxa's functional β-diversity ($R^2 = 0.54$, $p = 0.002$) and total community-weighted trait means ($R^2 = 0.43$–0.46, $p < 0.005$) are best explained by the same three environmental axes outlined in the above paragraph.

Although our data do not assess the timing of drivers on species presence, the three influential environmental gradients in the study are themselves tightly coupled and reshaped by Arctic warming: increased meltwater and primary-production pulses alter sediment grain-size distributions and organic content (sediment PC1/PC2), while rising temperatures and altered circulation patterns drive greater Atlantic-water intrusion, stratification shifts, and oxygen depletion (water PC1), and accelerating ice retreat reconfigures the spatial latitude–ice gradient (spatial PC2). Rather than reflecting the influence of a single environmental driver, these multivariate environmental gradients, together with trait convergence and the low functional diversity metrics identified in this study, point to the combined and interacting effects of multiple environmental filters that jointly constrain the range of viable trait strategies. Together, these interacting drivers likely act synergistically rather than independently, reinforcing environmental filtering and favoring a limited set of trait combinations.

Meanwhile, there were differences between dispersal-related traits and resource-use traits, with dispersal-related traits being most strongly associated with spatial gradients and sediment PC1, supporting the idea that mobile species are filtered by both geographic accessibility and sediments with higher mud and organic matter content. In contrast, resource-use traits (body size, living habit, feeding, and tolerance) were more strongly associated with sediment PC2 and water PC1, with both showing positive relationships with resource trait CWMs. This suggests that stations with a higher proportion of sand within an otherwise muddy composition, along with greater depth, higher salinity, and lower oxygen levels, support a broader range of feeding and living modes. Therefore, even when the traits are drawn from a relatively limited set, these patterns show how different aspects of species' ecological strategies are shaped by environmental filters acting at multiple scales.

Uniformly low functional diversity combined with high trait redundancy has important implications for ecosystem resilience and biogeochemical functioning in environmentally filtered systems such as the West Greenland shelf. Our data, which show trait convergence across Arctic, Boreal, and Cosmopolitan species, suggest that many ecosystem processes are currently supported by a relatively small number of functionally similar strategies. On the one hand, similar strategies, or trait redundancy, might mean processes such as sediment reworking, organic matter turnover, and carbon processing may remain relatively stable despite changes in species identity (Frid and Caswell 2015; Weigel et al. 2016; Douglas et al. 2017). On the other hand, while compensatory dynamics can occur among species sharing similar traits, the capacity to respond to novel or intensified disturbances may be limited if those disturbances selectively affect the dominant trait strategies (Biggs et al. 2020). In benthic systems, hypoxia, altered sediment dynamics, or shifts in organic matter supply have all been linked to abrupt functional change following the loss of key trait strategies (Frid and Caswell 2015; Törnroos et al. 2015). Consistent with observations from other Arctic benthic systems experiencing persistent physical and biogeochemical constraints (Sutton et al. 2021), trait redundancy can mask underlying vulnerability, as low functional diversity may reflect constrained adaptive capacity rather than resilience in Arctic benthic ecosystems undergoing rapid environmental change. Under continued climate forcing, further environmental change may therefore lead not to functional reorganisation, but to functional homogenization and potential loss of ecosystem-level processing, with consequences for benthic-pelagic coupling and long-term carbon processing (Kortsch et al. 2012; Frainer et al. 2021; Sutton et al. 2021). The convergence on a narrow trait space, with consistently low Rao's *Q* indicating limited trait dispersion across assemblages, may therefore reflect not only a potential future trajectory but a system in which functional homogenization has already occurred in response to long-standing environmental filtering and disturbance (Frainer et al. 2021). From a conservation perspective, these findings indicate that the presence of ecosystem functions alone may be an incomplete indicator of resilience, as limited trait diversity supporting those functions could constrain benthic communities' ability to adjust to further environmental change.

4.2 | Observation 1: The Boreal Group Exhibited Greater Trait Variability but Still Conformed to Dominant Trait Profiles

Despite the Boreal group exhibiting greater species richness, abundance and within-group trait variability, expressing a broader range of ecological strategies such as scavenging, predation, and varied living habits compared to the Arctic and Cosmopolitan species, it did not translate into higher functional richness or diversity at the community level. Warming of bottom waters by over 1°C since 1990 (Renaud et al. 2015) may have expanded suitable habitat for Boreal species, explaining their elevated richness and abundance in this region. Yet, our finding of low functional richness and diversity suggests that many of the traits observed among Boreal taxa overlapped with those already present in the community or were expressed by less abundant species, resulting in a limited overall functional trait space (low richness and trait dominance). This is also supported by our Boreal group β-diversity results of ~60% nested traits and ~40% turnover traits between stations. In this context, Boreal species may introduce taxonomic diversity and trait variability within their group, but the overall benthic assemblage remains functionally convergent due to the strong environmental filtering (Violle et al. 2007; Sutton et al. 2021).

4.3 | Observation 2: Clear Trait Differences Between Arctic and Cosmopolitan Species

When considering non-dominant traits, we found clear distinctions that may confer ecological advantages under varying environmental conditions. While differences existed among all three biogeographic groups, the sharpest contrasts were between Arctic and Cosmopolitan taxa, with Boreal species displaying more variable profiles (see Observation 1). The main distinctions were larval development mode (benthic/direct in Arctic species vs. pelagic/planktotrophic in Cosmopolitan and many Boreal taxa) and body size (small to small-medium in Arctic taxa and medium to large in Cosmopolitan taxa) (Figure 3). High-latitude benthic assemblages are widely recognised to favour non-planktonic development because of short productive seasons and harsh conditions reduce pelagic larval survival (Thorson 1959; Fetzer 2004). Conversely, the temperature–size rule predicts larger body sizes in colder environments (Atkinson 1995), but this relationship is not consistently supported by observations from Greenlandic benthos, based on both the present study and Armitage et al. (2025), likely because infaunal growth is constrained, not only by temperature, but also by sediment structure, oxygen limitation, and resource availability. With evidence of regional warming (Rantanen et al. 2022) and given that Cosmopolitan distributions were strongly associated with hydrographic (PC1) and spatial (PC2) gradients (i.e., dispersal processes), their expansion may intensify competition with Arctic and Boreal taxa for space and resources. Larger, planktotrophic Cosmopolitan species are therefore likely to hold advantages in resource acquisition and resilience to disturbance, enhancing their competitive ability in a changing Arctic compared with smaller, direct-developing Arctic taxa found in this study (Norkko et al. 2013; Séguin et al. 2014; Brose et al. 2016; Williams et al. 2025). To clarify the degree of intergroup competition and potential ecological displacement, future research should examine differences in feeding capacity, metabolism, and reproductive dynamics. Such insights would help identify which groups are most resilient or vulnerable, and reveal how redistribution of taxa may reshape benthic ecosystem processes such as organic matter cycling, nutrient flows, and benthic–pelagic coupling (Kristensen et al. 2012; Griffiths et al. 2017; Solan et al. 2020).

4.4 | Observation 3: Spatial Shifts in Species Abundance and Community-Weighted Trait Means Were More or Less Prominent at Particular Stations, Highlighting Areas of Greater Environmental Disturbance

The combination of biodiversity and functional metrics across space, along with species and trait contributions to β-diversity components, highlights spatial differences in environmental favourability and stress. Disko Bay represents the most disturbed part of our study area, with the world's largest depositing glacier driving extreme sedimentation, strong currents, and stratification (Gougeon et al. 2017). At the glacier-proximal stations (5 and 6), patterns of species composition and trait expression provided insights into tolerance and resilience. Station 5 (474 m) was mollusc-dominated, with Arctic and Boreal species contributing to roughly equal numbers, though Arctic taxa were more abundant. Station 6 (253 m) was dominated by annelids and Boreal taxa and showed the highest species abundance of all sites. Cosmopolitan species were scarce at both stations and contributed little to abundance or functional diversity, consistent with their overall decline at higher latitudes. Trait-based metrics revealed that high tolerance was the strongest signal in these communities, particularly at stations 5–7, where it peaked in both Arctic and Cosmopolitan groups. At Station 6, this pattern was driven almost entirely by the Arctic bivalve *Yoldiella solidula*, a species known to tolerate unstable, sediment-laden habitats in Arctic fjords (Włodarska-Kowalczuk et al. 2012). This supports the interpretation that tolerance traits are critical for persistence under glacier-driven disturbance, whereas Cosmopolitan taxa appear less resilient under such extreme environmental stress.

5 | Implications for Conservation and Future Perspectives

Our findings reveal that conserving Arctic benthic ecosystems can no longer rely on preserving regionally endemic species or fixed biogeographic boundaries, because the West Greenland shelf already functions as a system where Arctic, Boreal, and Cosmopolitan taxa coexist and share similar ecological roles. This convergence of traits, while reflecting strong environmental filtering, also implies that ecosystem functioning is maintained by a narrow set of strategies, making the system susceptible to further simplification (if not already limited) under disturbance or exploitation. In this context, conservation should prioritise the maintenance of functional complementarity (i.e., the diversity of ecological roles) rather than species identity alone. Given the region's economic importance for northern shrimp and Greenland halibut fisheries (and the associated by-catch of cod, snow crab, grenadiers, and wolffish), an ecosystem-based management approach that integrates infaunal processes and their compensatory or coexisting functions (Williams et al. 2025) would offer a more realistic safeguard of benthic resilience. Ultimately, sustaining biodiversity in a mixed Arctic–sub-Arctic system may not mean opposing species redistribution, but conserving the functional pathways that maintain ecosystem processes and consequently provide ecosystem services such as fisheries and carbon sequestration.

6 | Conclusions

Our findings reveal a taxonomically diverse yet functionally constrained benthic community along the West Greenland shelf, structured by overlapping biogeographic groups and strong environmental filtering. The presence of cosmopolitan species in the more northerly, colder regions suggests northward expansion of taxa typically associated with Boreal waters (Burrows et al. 2011; Poloczanska et al. 2013; Pinsky et al. 2020). These patterns may reflect climate-driven redistributions in Arctic ecosystems (Kuletz et al. 2024), but it remains uncertain whether such mixed communities are recent or long-standing, and what their composition implies for ecological processes such as food webs, fisheries, and carbon sequestration (Kristensen et al. 2012; Griffiths et al. 2017; Solan et al. 2020). Although functional redundancy exists for some traits, the overall lack of functional diversity suggests reduced ecological resilience and heightened vulnerability to pressures such as mining, fishing, and climate change. However, low functional diversity may also arise from natural spatial variability (e.g., sediment input, food supply), underscoring the need to disentangle long-term change from background environmental heterogeneity. To achieve this, future monitoring efforts should explicitly integrate taxonomic and trait-based metrics, track shifts in dominant functional roles (e.g., feeding mode, mobility, body size), and couple benthic observations with key physical and biogeochemical drivers such as sediment characteristics, oxygen conditions, and carbon or nutrient fluxes. Beyond documenting change through time, such approaches should also enable a deeper understanding of intra- and interspecific variability in ecosystem functioning, including whether Arctic, Boreal, and Cosmopolitan species contribute equally or differently to key processes such as organic matter processing, carbon sequestration, and benthic–pelagic coupling. Integrative, long-term datasets that resolve functional traits at higher ecological resolution are therefore essential for improving predictive models of benthic functional change, identifying early signals of functional homogenization or loss (or gain) of response diversity, and anticipating consequences for ecosystem functioning and services in Arctic shelf ecosystems undergoing rapid environmental change.

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Disclosure

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Ethics Statement

The authors have nothing to report.

Consent

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data used in this study are publicly available on Zenodo under a Creative Commons Attribution (CC BY 4.0) licence. The repository includes the processed biodiversity and trait datasets, and all supporting materials required to reproduce the results. The dataset can be accessed at: https://doi.org/10.5281/zenodo.19451826.

Peer Review

For transparency, the peer review documents associated with this article are available at https://doi.org/10.1111/ddi.70195.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Heat map of Arctic species abundance across stations. Rows represent species and columns represent stations. Hierarchical clustering is shown for both species and stations. Colour intensity reflects abundance values. **Figure S2:** Heat map of Boreal species abundance across stations. Rows represent species and columns represent stations. Hierarchical clustering is shown for both species and stations. Colour intensity reflects abundance values. **Figure S3:** Heat map of Cosmopolitan species abundance across stations. Rows represent species and columns represent stations. Hierarchical clustering is shown for both species and stations. Colour intensity reflects abundance values. **Figure S4:** raw plots of the trait community weighted means for each trait and its categories shown over latitude. Yellow represents the Arctic group, orange is the Boreal group, and red is the Cosmopolitan group. **Figure S5:** i) Total correlations between all environmental variables, and therefore, the justification for using PCA axes in explaining differences in sediment characteristics, water properties and spatial gradients. ii) shows the final environmental PC axes used in the analysis with no correlations over 0.6, justifying their use in the final models and ability to explain different information. **Figure S6:** Main PCA axis (i) and Scree plots (ii) for A) Sediment, B) water characteristics and C) spatial gradients variables. The Scree plots of PCAs justify selected PCA axes as variables in the MRM environmental analysis. **Table S1:** Completeness of trait assignments across taxa used in trait-based analyses. Trait completeness was calculated as the proportion of taxa with non-zero fuzzy-coded scores across the modalities of each trait. Coverage was high for most traits, with lower completeness for tolerance-related traits. **Table S2:** Trait matrix for all taxa included in the analyses of the main text. Taxa are coloured according to biogeographic classification (Polar, yellow; Boreal, orange; Cosmopolitan, red). Trait categories were assigned using fuzzy coding. Shaded trait cells indicate cases where trait information was unavailable. **Table S3:** The five most and the five least common trait categories as identified by the highest-scoring (left) trait affinity matrix and lowest (or no) affinity (right) for each biogeographic group and the total community. Inside the brackets is the average affinity score according to the fuzzy coding approach, followed by the percentage of the species that have an affinity to the score (e.g., 53% of the species in the Arctic group have some level of affinity to benthic/direct larvae development). Averaged affinity scores and percentages are rounded to 1dp and 0dp, respectively. Traits in bold text in the biogeographic groups are those that are different from the Total community. **Table S4:** Model statistics from Multiple Regression on distance Matrices (MRM) analyses. Left: repeat of main Figure 7 from the main text for context. Middle: Statistics corresponding to the model coefficients (shaded cells) of the best-fitting composite environmental dissimilarity models, showing variance explained (R^2), significance levels, and selected environmental gradients for each response variable (taxonomic β-diversity, functional β-diversity, and trait-based community-weighted means). Right: Statistic table or individual environmental variables tested in MRM analyses (asterisks overlaid on the heatmap), including regression coefficients (β), significance levels, and the contribution of each predictor variable to community dissimilarity. Grey colour denotes non-significant results. **Appendix S2:** Determination of water content, organic and carbonate content in marine sediments by Loss On Ignition (LOI). **Appendix S3:** Methods for sample preparation before sedigraph analysis by Peter Osterholm.

Paper III

From surface flux to seafloor function: vertical carbon export and benthic communities in high-latitude coastal systems

From surface flux to seafloor function: vertical carbon export and benthic communities in high-latitude coastal systems

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Abstract

The downward flux of carbon from the surface ocean to the seafloor fuels benthic invertebrate biomass and drives carbon sequestration. In polar regions, pelago-benthic carbon coupling is shaped by complex processes influenced by climate change, including glacial retreat, water stratification, and warming. Here we examine three high-latitude coastal systems along the Northeast Greenland coast: Dove Bugt, the Brede–Ardencaple Fjord system, and Kong Oscar Fjord, each differing in bathymetry, glacier influence, and exposure to Atlantic Water at depth. Using short-term sediment-traps, hydrographic profiling, sedimentary carbon analyses, and trait-based macrobenthic community data, we assess how vertical particulate organic carbon (POC) export, sedimentary organic carbon stocks (SOC), and benthic biomass and function are linked across the three coastal systems. We found that vertical POC flux and SOC were highly variable in space and showed no consistent relationship with benthic invertebrate carbon biomass. Our trait analysis of the benthic communities revealed that only a subset of trait strategies, particularly only epifaunal suspension feeders, consistently translated carbon availability into standing biomass. Latent variable modelling, which identifies underlying ecological gradients not explained by measured environmental predictors, revealed an additional axis structuring benthic trait biomass and is most consistent with bathymetric relief and associated horizontal redistribution processes. Thus, with our results showing a temporal decoupling among POC export, SOC, and benthic carbon biomass, we propose that future research investigate lateral transport pathways associated with Atlantic Water intrusion and stratification, alongside benthic production and ecosystem functioning, to better understand carbon processing, retention, and sequestration in Arctic systems.

1 Introduction

Vertical carbon flux from the surface ocean to the seafloor is a central process structuring benthic ecosystems, regulating biogeochemical cycling, and carbon storage in marine environments (Piepenburg 2005; Griffiths et al. 2017; Solan et al. 2020). This export is especially critical in the Arctic, where the efficient transfer of organic matter during highly seasonal production periods contributes to tight pelagic–benthic coupling (Clarke 1983; Piepenburg 2005; Wiedmann et al. 2020). Pulses of organic material can rapidly reach the seafloor, creating seasonal hotspots of benthic activity, with infaunal and epifaunal invertebrates responding to both the magnitude and timing of export (Grebmeier et al. 2015; Sen et al. 2024). As Arctic benthic communities play a key role in the transformation, storage, and remineralisation of this carbon (Griffiths et al. 2017; Solan et al. 2020), changes in export efficiency of organic material, degradation state, and mode of transfer can restructure benthic biomass, food web pathways, and carbon cycling (Yool et al. 2017; Kiesel et al. 2020; Yunda-Guarin et al. 2020)

Across Arctic shelves, declining sea-ice cover increases light availability and enhances primary production in surface waters (SW) (Arrigo et al. 2008; Michel et al. 2015; Lewis et al. 2020). Increased primary production in SW, however, does not necessarily translate into enhanced carbon export to the seafloor. Export magnitude and quality depend strongly on water-column structure, particularly stratification and nutrient resupply, both influenced by the increasing intrusion of warm Atlantic Water (AW) onto shelves and into fjord systems (Sejr et al. 2017; Wiedmann et al. 2020; Gjelstrup et al. 2022). AW shoaling has intensified across Arctic regions (Gjelstrup et al. 2022), and while it is ultimately a consequence of broader climate-driven changes, its presence inside fjord coastal systems is also driven by coastal seafloor topology and glacier type influences (Arndt et al. 2015; Hill et al. 2017). Unlike terrestrial-terminating glaciers, marine-terminating glaciers promote subglacial discharge and buoyancy-driven plumes that draw AW into inner fjords, enhancing circulation and modifying stratification (Straneo and Heimbach 2013; Hill et al. 2017; Meire et al. 2017). When water mixing is limited and strong vertical stratification persists (such as in terrestrial-terminating glaciers), it may limit vertical nutrient resupply and promote retention and recycling of organic matter in the upper water column, altering not only the quantity but also the quality and timing of organic matter reaching the seabed (Bridier et al. 2021a; Von Appen et al. 2021; Bodur et al. 2024). As many marine-terminating glaciers in Northeast Greenland are retreating across bathymetric highs and transitioning toward terrestrial termination (Hill et al. 2017; Wood et al. 2021), associated changes in circulation and stratification are likely to influence carbon delivery pathways and benthic communities dependent on downward carbon flux (Wiedmann et al. 2020; Bao and Moffat 2024; Sen et al. 2024).

Beyond traditional measurements of carbon export, hydrography, and benthic communities, trait-based approaches provide a mechanistic framework for understanding how organic carbon is processed and retained at the seafloor (Beauchard et al. 2017; Degen et al. 2018; Wiedmann et al. 2020; Estapa et al. 2021). Different benthic strategies access carbon through distinct pathways: epifaunal suspension feeders primarily intercept advected and vertically delivered particulate material, infaunal deposit feeders exploit sedimented organic matter within the seabed, and mobile predators and scavengers integrate carbon indirectly through trophic transfer. The relative importance of these pathways is not fixed, but shaped by environmental conditions, with glacier-proximal, high-turbidity systems tending to favour tolerant deposit-feeding infauna, while outer fjord and shelf environments support suspension feeders reliant on both vertical and lateral inputs (Sejr et al. 2000; Węsławski et al. 2011; Cummings et al. 2021). Conversely, under strongly stratified conditions with reduced delivery of particulate organic matter, communities may shift toward strategies adapted to lower carbon supply (Pineda-Metz et al. 2020; Komendić et al. 2024). These environmentally structured differences in carbon acquisition pathways influence not only how carbon is accessed, but also how it is retained within biomass, redistributed within sediments, or transferred through food webs, such that variation in trait composition can impact both the magnitude and residence time of carbon at the seafloor (Barnes and Sands 2017; Morley et al. 2022), a component rarely captured in regional carbon budgets (Ehrnsten 2020). In highly seasonal Arctic systems, where short-lived production pulses must sustain benthic communities through prolonged periods of low input (Clarke 1983; Renaud et al. 2020), this linkage becomes particularly important: communities with diverse feeding modes and trophic levels indicate greater biological mediation of carbon flow and enhanced functional resilience (Degen et al. 2018; Liu et al. 2019; Hinz et al. 2021), highlighting that trait composition not only reflects environmental conditions but actively governs how carbon is utilised and maintained within benthic ecosystems (Degen et al. 2018; Armitage et al. 2025).

In this study, we investigate three glacially influenced coastal systems along the Northeast Greenland coast (72–76° N, 16–25° W): (i) the Dove Bugt embayment, characterised by a broad, trough-dominated shelf embayment with strong tidal mixing, and relatively high seasonal productivity; (ii) a fjord transect spanning inner to outer regions of the connected Brede Fjord and Ardencaple Fjord system, where sill-mediated circulation and glacier-proximal basins create pronounced hydrographic and depositional gradients; and (iii) an inner channel of the Kong Oscar Fjord complex, a deeper fjord system influenced by stratified AW inflow at depth (Meire et al. 2017; Gjelstrup et al. 2022; Koski 2026). We combine water column sediment trap measurements, water column hydrographic profiling, bathymetric data, and benthic community surveys to examine how carbon flux, water column structure (including AW), and bathymetry (*e.g.*, sills that may restrict AW penetration into inner fjords) together relate to carbon with benthic invertebrate biomass and functional composition. We combine sediment trap measurements at 5 to 7 depths, hydrographic profiling, bathymetric data, and benthic community surveys to examine how carbon flux, water-column structure, and seafloor topography interact to influence benthic biomass and functional composition. Specifically, we ask: (1) how does water-column structure vary among systems, and how do bathymetry and fjord geometry influence AW penetration? (2) How does variation in stratification relate to vertical POC flux and sedimentary carbon stocks? (3) How do different carbon pathways (vertical export versus sedimentary stocks) relate to benthic invertebrate biomass and trait composition? (4) Do carbon-related variables, such as water column particulate organic carbon (POC) and sedimentary organic carbon (SOC), emerge as primary drivers of benthic community structure relative to other environmental factors? Together, these questions evaluate pelagic–benthic coupling across contrasting glacial systems and identify the mechanisms regulating benthic carbon utilisation and functional organisation.

2 Methods

2.1 Study area and sampling context

The study area lies within the Northeast Greenland National Park, a largely unaltered high-Arctic region that provides a rare natural laboratory for examining how AW intrusion and glacial retreat shape carbon pathways and benthic ecosystem functioning. All the data were collected from three coastal systems influenced by marine-terminating glaciers: Kong Oscar Fjord, Brede/Ardencaple Fjord (hereafter referred to as Ardencaple Fjord), and Dove Bugt. These systems differ in fjord structure, sill depth, and exposure to AW, and all have varying degrees of freshwater input from glacial melt and terrestrial runoff. The region is strongly influenced by interactions between the East Greenland Current, which transports cold Polar Water (PW) southward, and incursions of warmer, saline AW from the Return Atlantic Current in the North and the Irminger Current in the South. These hydrographic contrasts influence stratification, sedimentation, and benthic habitat structure.

Sampling stations were arranged to capture gradients from glacier-proximal to outer fjord and shelf-influenced environments. In Dove Bugt, two stations (DB1–DB2) were situated in the inner and central regions of the embayment. In the Ardencaple Fjord system, four stations (ACF1–ACF4) spanned from the inner fjord basin near the glacier to the outer fjord region. In Kong Oscar Fjord, three stations (KOF1–KOF3) progressed from enclosed inner settings toward more open, shelf-influenced conditions. This sampling design captures gradients in glacial influence, bathymetry, and hydrographic connectivity.

2.2 Macrofauna sampling procedures

Macrobenthic infaunal samples were collected aboard R/V *Maria S. Merian* in August 2022. Samples were collected using a box corer (1000 cm^2), sieved through a 1 mm mesh, and preserved in 70% ethanol for identification at Åbo Akademi University and the Institute of Oceanology, Polish Academy of Sciences. Nine stations were sampled with three replicates each, and data were standardised to m^2. Macrofaunal biomass (wet weight) was converted to carbon biomass following Rowe et al. (1994) and Wiedmann et al. (2020) assuming 4.3% of wet weight as carbon. Owing to data heterogeneity, carbon biomass values were fourth-root transformed before analysis. Phyla composition of benthic biomass and cumulative biomass across sampling stations is shown in Supplementary Material (SM), Fig. S1.

2.3 Macrofauna traits

Three traits (feeding habit, mobility, and environmental position) were extracted from the Arctic Trait Database (Degen et al., 2019; https://arctictraits.univie.ac.at). These traits were chosen for their relevance to benthic carbon pathways (Węsławski et al. 2011; Pineda-Metz et al. 2020; Cummings et al. 2021; Komendić et al. 2024). Trait information was gathered utilising the fuzzy-coding approach from the Arctic Trait Database, which allows species to express multiple trait modalities. Fuzzy scores were converted to categorical labels to retain species-level trait identities, with species assigned to one or more modalities where appropriate (e.g. burrower–crawler). Species-level carbon biomass values were then linked to their corresponding trait modalities to construct a trait–carbon biomass matrix for each station. To reduce noise from rare traits and low-biomass taxa, the dataset was truncated to retain trait modalities representing 95% of total macrofaunal biomass. The full distribution of trait assignments prior to truncation is provided in SM Fig. S2. The resulting matrices were used for all subsequent species- and trait-based analyses.

2.4 Environmental parameters

2.4.1 Sediment grain size and sedimentary organic (carbon) material

For each box core replicate, two additional sediment subsamples were collected for physical and chemical analyses using 50 mL Falcon tubes inserted vertically ~10 cm into the sediment to capture both surface and subsurface layers. Carbon and nitrogen concentrations were quantified at Tvärminne Zoological Station (University of Helsinki) using a Europa Scientific ANCA-MS 20-20 mass spectrometer. Grain size composition was analysed at Åbo Akademi University following hydrogen peroxide oxidation to remove organic matter. Fine fractions (<63 µm) were quantified using the SediGraph technique, enabling determination of silt and clay distributions (SM Fig. S3).

2.4.2 Seafloor bathymetry and transect profiling

Multibeam bathymetric data were collected using a Kongsberg EM122 echosounder system aboard the same R/V *Maria S. Merian* expedition (Thomas et al. 2024). Raw data were processed onboard using standard calibration procedures, including sound velocity corrections and manual removal of noise artefacts. Further refinement was carried out using QGIS (v3.28; bathymetry and hillshade shown in SM Fig. S4). Bathymetric profiles were extracted along transects originating at the innermost station of each coastal system, with seafloor depth plotted relative to cumulative transect distance.

2.4.3 Carbon flux and water profiling

Hydrographic profiles were collected using a Seabird SBE 911plus CTD. The instrument was calibrated pre-cruise and sampled at 24 Hz. Data were processed following TEOS-10 standards to derive salinity, potential temperature (θ), and potential density anomaly ($\sigma\theta$) and binned to 1 dbar intervals. Temperature–salinity diagrams were used to identify Surface Water (SW), Polar Water (PW), and Atlantic Water (AW) masses, which were classified using conservative thresholds for salinity and potential temperature: SW (salinity 15–30, θ = 0–7.5 °C), PW (salinity 26–34, θ = –2 to 2 °C), and AW (salinity 34–35.1, θ = –1 to 4 °C) (Gjelstrup et al. 2022).

Short-term sediment trap deployments were conducted at seven stations across the three coastal systems in Northeast Greenland: Dove Bay (1 station), Ardencaple Fjord (3 stations), and Kong Oscar Fjord (3 stations). Bottom-moored arrays equipped with 2–4 transparent plexiglass cylinders (KC Denmark, 72 mm inner diameter; aspect ratio 6.25) were deployed at 5-7 depths, typically including 20, 30, 50, 90, 120, and occasionally 200 and 400 m, for ~22 hours. Each cylinder was pre-filled with GF/F filtered seawater adjusted to a salinity of ~40 to reduce turbulence upon particle entry. Samples were processed for POC and PON following filtration (100–300 ml) and stored at 4°C. Data were published by Wiedmann and Svensen, 2024: https://doi.org/10.11582/2024.00040, 2024).

To estimate POC flux at the seafloor, station-specific attenuation coefficients were derived from log–log regressions of sediment trap POC flux data against depth. Seafloor flux was calculated relative to the deepest measured trap using the fitted attenuation coefficient and the ratio between seafloor depth and deepest trap depth. This approach minimises extrapolation and provides conservative estimates of carbon delivery to the benthos.

2.5 Data analysis

2.5.1 Handling environmental variables

For all environmental variables, including depth, bottom-water properties (temperature, salinity, oxygen, fluorescence, turbidity), and carbon-related variables (POC flux, sediment organic carbon, and C:N ratios), we calculated mean, standard deviation, and coefficient of variation (CV) across stations (SM, Fig. S5; Table S6). CV analysis was used to assess relative variability among environmental variables and to identify those with the greatest variation across stations. Depth exhibited moderate variability ($CV \approx 40\%$), while salinity and oxygen were relatively stable ($CV < 5\%$). Temperature, fluorescence, and turbidity showed high CVs (>79%); however, this reflected low absolute values rather than large absolute variation (Table S6). Strong covariance among environmental and carbon variables indicated substantial multicollinearity (SM, Fig. S7), suggesting that several predictors shared information rather than representing independent processes.

To avoid unstable parameter estimates and retain mechanistically interpretable predictors, we restricted the final model to variables describing carbon delivery and storage at the seabed. Specifically, we extrapolated the POC flux measurement from the deepest sediment trap as a measure of downward carbon supply and sediment organic carbon (SOC) as a measure of surface sediment carbon stock. Flux C:N, sediment C:N, and depth were excluded due to strong covariance with other predictors. All retained variables were z-score standardised prior to analysis. To test whether benthic biomass and trait composition respond most strongly where pelagic delivery and benthic storage align, we additionally included a vertical POC flux × SOC interaction term.

2.5.2 Generalised linear latent variable modelling approach

Generalised Linear Latent Variable Models (GLLVMs) are a model-based framework for multivariate data that combines regression and ordination approaches. Measured predictors account for observed environmental effects, while latent variables capture residual correlations among species and trait biomass distributions, representing community-wide responses to unmeasured ecological or environmental gradients. In this framework, latent variables (the model's output) therefore represent unmeasured ecological or environmental gradients associated with processes not captured by the measured predictors.

Models were fitted using a Tweedie distribution, appropriate for continuous biomass data containing zeros (SM, Fig. S8 & S9), using the R package *gllvm* (Niku et al., 2019). Models with zero to three latent variables were fitted and compared using

Akaike's Information Criterion (AIC). Although AIC decreased with additional latent variables, models with two and three latent variables showed poor convergence and near-zero variance in additional axes, indicating over-parameterisation (SM, Tables S10i–iii). A single-latent-variable model was therefore selected as the most parsimonious and interpretable solution. We additionally evaluated whether the coastal system (*e.g.*, DB, ACF, or KOF) should be included as a categorical random effect to account for the hierarchical structure among stations. Yet, their inclusion did not improve model fit and explained negligible variance (SM, Table S10iii) and was therefore excluded. The final model included POC flux and SOC as fixed effects, along with a single latent variable capturing residual structure. Model adequacy was evaluated using Dunn–Smyth residual diagnostics, which showed no major violations, homoscedasticity, or systematic patterns across stations or trait biomass.

2.5.3 Post-hoc analyses of the latent variable gradient

To interpret the latent variable, site scores from the first latent axis (LV1) were related to environmental, bathymetric, and community metrics using linear models. Predictors included bottom-water properties, distance from glacier, carbon flux and SOC variables, and bathymetric descriptors (slope, aspect, and terrain ruggedness; Section 2.4.2). To assess links with benthic community organisation, complementary functional diversity metrics were calculated from the trait-based carbon biomass matrix using the *vegan* package (Oksanen et al., 2022). Metrics included functional richness (defined as the number of distinct trait categories represented at each station), Shannon and Simpson diversity, Hill numbers (Hill 1 and Hill 2), and Pielou's evenness. Each metric was analysed separately against LV1. Model coefficients, R^2 values, and significance levels were extracted to evaluate relationships between the latent gradient and environmental and community variables. All analyses were conducted in R (R Core Team, 2024) using RStudio (version 2024.12.0).

3. Results

3.1 Physical environment and water-mass structure

The water depth ranged from 50 m at the shallowest sill to approximately 600 m in Ardencaple and Kong Oscar Fjord; Dove Bugt is considerably shallower, reaching approximately 400 m with sampling stations at approximately 200 m. All three coastal systems showed a consistent three-layer water-mass structure composed of surface meltwater and PW overlying AW (Fig. 1). AW was present at the seafloor at every station, regardless of location to glacier, sill depth or local basin morphology (Fig. 1). Consequently, bottom-water temperature, salinity and oxygen showed limited spatial variation relative to the strong differences observed in carbon supply (SM, Fig. S5 & Table S6). All stations were comparable in sediment composition (~50% mud, ~40% silt, ~0-10% sand, and occasionally <5% gravel; SM, Fig. S3 & S5). Therefore, we conclude that stations within and among these three systems experience broadly comparable seafloor physical conditions in terms of bottom-water properties and sediment composition.

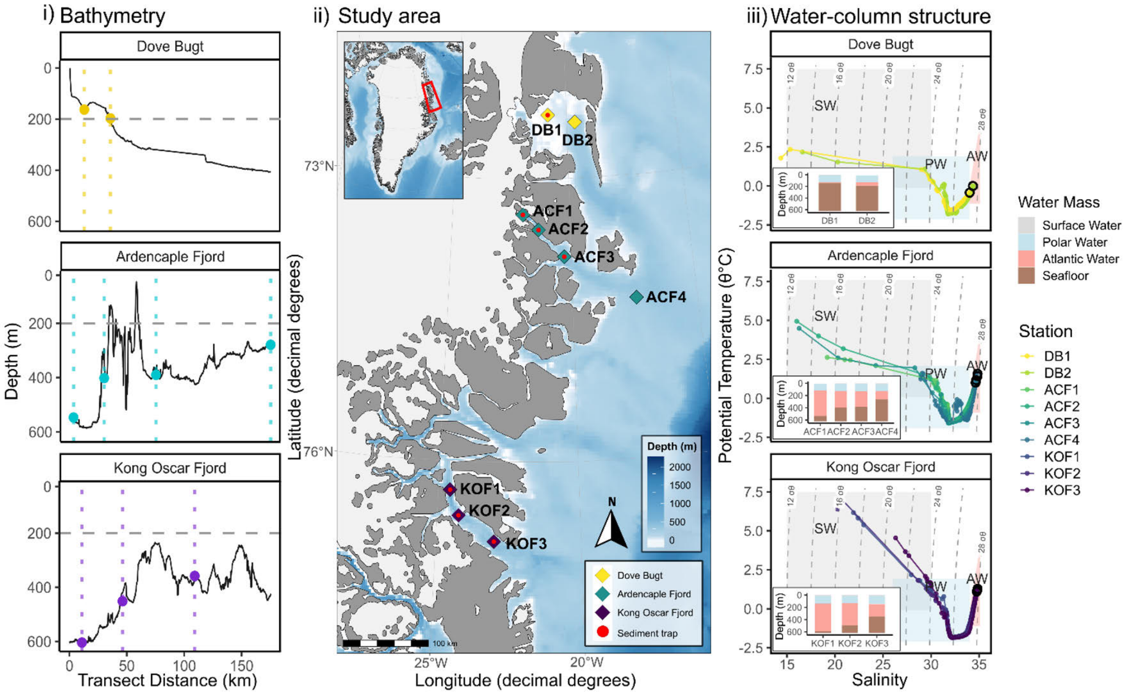

Figure 1 | Bathymetry (i), location of stations in the study area (ii), and water-mass structure (iii) across three Northeast Greenland coastal systems. **(i):** Bathymetric profiles derived from multibeam data for each system, with sediment trap and benthic sampling depths indicated with coloured dots relative to the coastal system **(ii):** Map showing the locations of benthic sampling stations in Dove Bugt (DB1–2), the Ardencaple Fjord system (ACF1–4), and Kong Oscar Fjord (KOF1–3), overlaid on regional bathymetry. **(iii):** Temperature–salinity (T–S) diagrams for each fjord system, showing potential temperature versus salinity for all CTD casts. Isopycnals of potential density (σθ) are overlaid. Water masses are classified as SW (Surface Water), PW (Polar Water), and AW (Atlantic Water). Black circles indicate bottom-water conditions at benthic sampling depths. Smaller inserts: Stacked bars as vertical distribution of major water masses along transects in three Northeast Greenland coastal systems, with seafloor depth indicated in brown.

3.2 Spatial variation in particulate organic carbon flux and sedimentary organic carbon

The vertical export of POC varied among stations and depth (Fig. 2). At all stations, POC export was highest in the upper water column (SW) and declined with depth, with a marked change in attenuation slope typically occurring between ~100 and 200 m, coinciding with the transition to Atlantic Water (AW) (Fig. 1, 2).

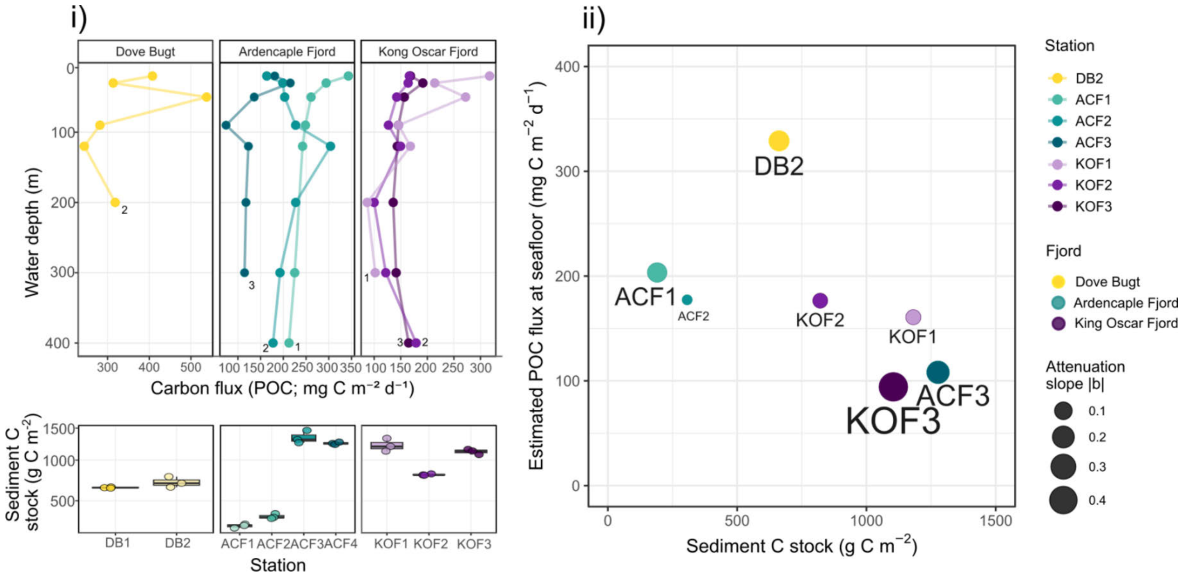

Figure 2 | Spatial variation in vertical carbon export, sediment organic carbon (SOC), and attenuation across the coastal systems. (i) Profiles of particulate organic carbon (POC, mg C m^{-2} d^{-1}) flux to the seafloor for each coastal system, shown as a function of depth. Colours denote systems (Dove Bugt, Ardencaple Fjord and Kong Oscar Fjord). Lower panels show surface SOC concentrations for each station (g C m^{-2}). (ii) Relationship between SOC (g C m^{-2}, x axis; log scale) and estimated POC flux at the seafloor (mg C m^{-2} d^{-1}, y axis; log scale). Symbols indicate the coastal system, coloured by transect position (inner, middle, outer). Symbol size denotes the attenuation slope |b|.

Across the three coastal systems, the vertical POC export reaching the seafloor showed relatively moderate variation (threefold) among stations (~110 to ~320 mg C m^{-2} d^{-1}), indicating broadly comparable levels of vertical carbon supply despite small-scale differences in POC export and attenuation (Fig. 2ii). Dove Bugt, the shallowest of the three systems and therefore subject to reduced attenuation during sinking, exhibited the highest vertical POC export at depth (318.3 mg C m^{-2} d^{-1}), compared to the Ardencaple Fjord and Kong Oscar systems, which averaged 168.2 ± 49.5 and 148.5 ± 41.0 mg C m^{-2} d^{-1} (mean ± SD), respectively. Attenuation-corrected estimates of POC export arriving at the seafloor (Fig. 2ii) remained broadly similar to POC export measured in the deepest sediment traps, as there were often relatively short distances and limited attenuation between the deepest trap and the seafloor across stations (SM, Figure 11i & Table S11ii).

Within coastal systems, there is evidence of spatially structured vertical POC export. In the Ardencaple Fjord system, vertical POC export in the deepest traps declined from the inner fjord (212.4 mg C m^{-2} d^{-1}), through the mid-fjord station (177.3 mg C m^{-2} d^{-1}), to the outer station near the fjord mouth (114.7 mg C m^{-2} d^{-1}). In Kong Oscar Fjord, POC export followed a similar pattern to Ardencaple Fjord, with values around 170 mg C m^{-2} d^{-1} at the inner and middle stations, declining to 101.9 mg C m^{-2} d^{-1} at the outer, most open station.

Surface SOC exhibited clear location-specific patterns rather than a consistent inner–outer gradient across systems (Fig. 2). In the Ardencaple Fjord system, SOC increased markedly from the inner fjord (ACF1, 190.6 g C m^{-2}) through the mid-fjord station (ACF2, 306.6 g C m^{-2}) to the outer fjord stations (ACF3, 1,276.9 and ACF4, 1,206.5 g C m^{-2}), forming a pronounced spatial gradient. In contrast, Kong Oscar Fjord displayed a non-monotonic pattern, with relatively high SOC at KOF1 (1181.4 g C m^{-2}), lower values at KOF2 (821.3 g C m^{-2}), and elevated values again at KOF3 (1104.2 g C m^{-2}). SOC in Dove Bugt were comparatively uniform, with DB1 and DB2 exhibiting little spatial separation between stations (662.1 and 726.3 g C m^{-2}, respectively).

Surface sediment C:N ratios exhibited a clear spatial gradient across the study area, with higher values at glacier-proximal and inner-coastal stations and progressively lower ratios toward outer-coastal and shelf stations (SM, Fig. S12). This pattern was consistent across the investigated systems and suggests systematic variation in organic matter composition along the coastal gradient. As C:N covaried strongly with carbon flux and other environmental variables, it was not included as an independent predictor in the GLLVM analyses, but it provides context for interpreting spatial differences in carbon sources and processing at the seafloor.

Despite broadly comparable vertical POC export across stations, SOC showed no clear relationship with estimated seafloor carbon supply (export). For example, stations with high SOC, such as KOF1 (1,181.4 g C m^{-2}) and ACF3 (1,276.9 g C m^{-2}), were associated with moderate vertical POC export at the deepest trap depth (164.9 and 114.7 mg C m^{-2} d^{-1}, respectively), whereas KOF3 exhibited one of the lowest POC export measurements (101.9 mg C m^{-2} d^{-1}) despite a relatively high SOC content in the sediment (1104.2 g C m^{-2}). Conversely, stations with higher POC export at depth, such as DB1 (318.3 mg C m^{-2} d^{-1}), did not exhibit proportionally elevated SOC (726.3 g C m^{-2}).

3.3 Benthic biomass and dominant functional strategies

Across the region, nearly all benthic carbon biomass (≈ 95 %) was concentrated within a limited number of functional trait combinations defined by environmental position (infaunal vs epifaunal), feeding habit and mobility (Fig. 3). Infaunal deposit-feeding burrowers and epifaunal suspension-feeding crawlers and sessile taxa were the principal contributors to biomass across stations. Total benthic carbon biomass varied among stations, spanning more than an order of magnitude, with the highest values occurring where SOC was greatest (KOF2 & ACF3; SM Fig. S1).

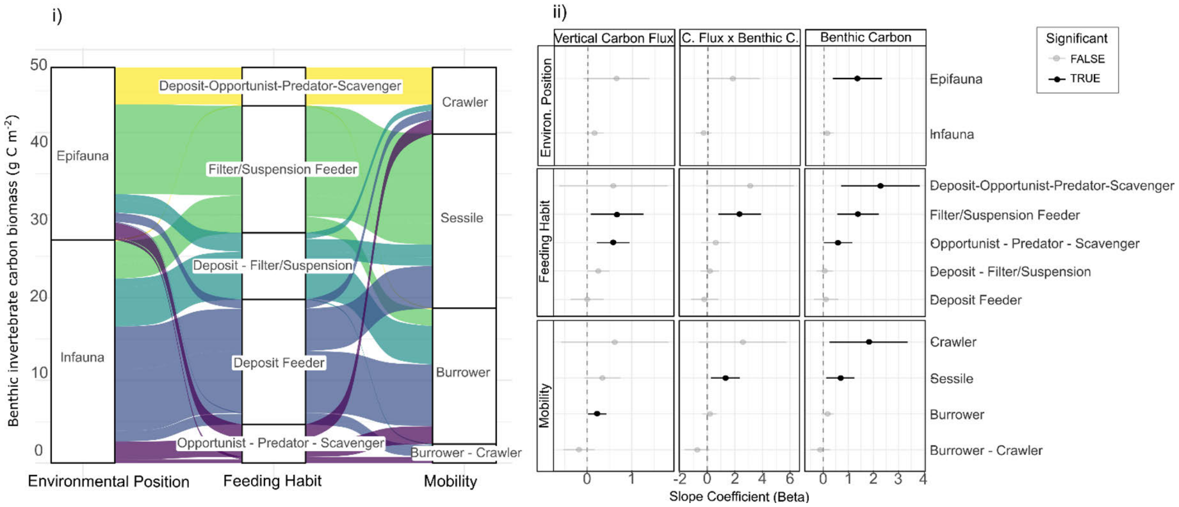

Figure 3 | Trait-based composition of benthic carbon biomass and trait-specific responses to carbon variables. (i) The distribution of benthic carbon biomass (g C m^{-2}) across major trait groups. Colours represent the proportional contribution of each trait combination to the total benthic invertebrate carbon pool. **(ii)** Trait-specific coefficients from the GLLVM models for three carbon predictors: vertical POC flux (export) (mg C m^{-2} d^{-1}) at the deepest sediment trap depth, the interaction between vertical POC flux and SOC, and surface SOC. Points represent estimated coefficients (β), with horizontal lines indicating 95% confidence intervals. Black points denote statistically significant effects at $P < 0.05$ (“true”), whereas grey points indicate non-significant effects at $P \geq 0.05$ (“false”). Panels are grouped by trait categories of environmental position, feeding habit and mobility.

Trait-specific GLLVM models revealed marked heterogeneity in how benthic invertebrate carbon biomass responded to the measured carbon variables (Fig. 3). Positive relationships with SOC were observed primarily for epifaunal trait groups, including sessile and crawling taxa, as well as for mixed opportunistic predator–scavenger strategies. Vertical POC export was associated with elevated biomass in a more restricted subset of traits, most notably epifaunal filter and suspension feeders. For these taxa, the interaction between POC supply and SOC produced the strongest coefficients, indicating the highest biomass where pelagic carbon delivery coincided with elevated benthic carbon pools.

In contrast, infaunal deposit feeders, burrowers, and deposit–filter feeding traits exhibited coefficients centred near zero across all carbon predictors, indicating no detectable relationship between daily POC supply and standing biomass for these functional strategies. Several additional trait groups showed weak or non-significant responses, highlighting substantial functional variation in how organic carbon is accessed and incorporated into benthic biomass. Across all traits, model residuals were structured along a single latent variable, indicating that a shared unmeasured gradient remained after accounting for the carbon predictors. This gradient is examined in the following section.

3.4 A latent hydrodynamic gradient shaping functional composition

Latent variable (LV) modelling identified a single residual multivariate gradient that persisted after accounting for POC flux and SOC. To explore its potential drivers, we examined relationships between LV scores and environmental and diversity metrics. None were statistically significant, and several predictors covaried strongly (particularly depth, temperature, and flux C:N; SM Fig. S13), limiting their independent interpretation. Nonetheless, moderate associations were observed for functional richness ($R^2 \approx 0.31$) and seafloor terrain metrics, including ruggedness and slope ($R^2 \approx 0.26$–0.33), with more structurally complex or exposed stations tending toward higher LV scores. Depth and sediment C:N showed weaker alignment ($R^2 \approx 0.18$), whereas flux C:N exhibited little correspondence ($R^2 \leq 0.04$). These patterns do not imply predictive relationships, but indicate that multiple, partly collinear gradients orient along the LV and contribute to the structure captured by the ordination.

The LV further separated stations into three broad groups (low, intermediate, and high scores; Figs. 4–6). When considered alongside benthic biomass, trait composition, and bathymetry, this gradient aligned with differences in seafloor topography and exposure. Stations with higher LV scores were associated with steeper or more exposed terrain, whereas lower scores corresponded to more enclosed basin settings. This pattern suggests that the LV likely captures variation in unmeasured hydrodynamic processes, including lateral advection, tidal mixing, and resuspension, that are not resolved by static environmental variables.

3.4.1 Low LV scores: depositional, disturbance-dominated environments

Stations with low LV values (*e.g.*, KOF1, ACF1) exhibited the lowest benthic invertebrate biomass among all stations (KOF1 biomass = 3.65 g C m^{-2} and ACF1 = 1.11 g C m^{-2}; Fig. 4). ACF4 had the lowest functional groups to any station (n=4), indicating reduced trait diversity and dominance of a limited set of feeding and movement strategies. Assemblages were dominated by infaunal deposit feeders, particularly at ACF1, while KOF1 showed a low representation of epifaunal suspension feeders, and both showed no mixed functional roles. Based on their position in the bathymetry, these environments likely experience frequent disturbance from deposition, sediment resuspension and near-bottom plume activity, resulting in a mechanically dynamic benthic habitat dominated by burrowing fauna.

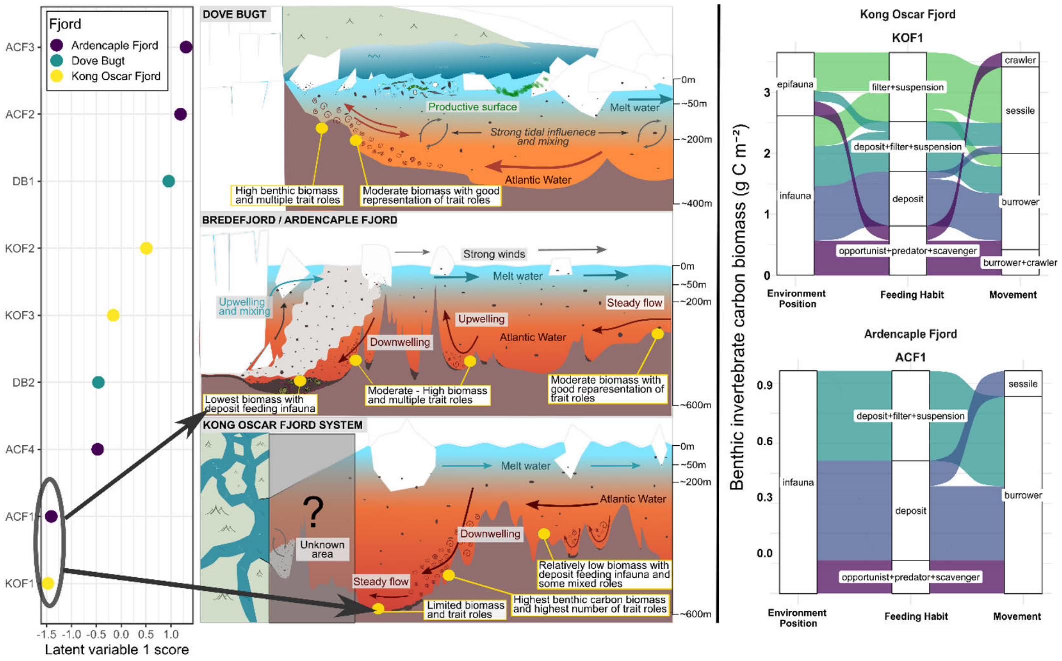

Figure 4 | Left panel shows station scores along the first latent variable (LV1), with stations coloured by coastal system. Stations with low LV scores (*e.g.*, KOF1, ACF1) cluster at the negative end of the gradient. Central panels illustrate conceptual depositional and disturbance-dominated inner-fjord settings characterised by high sedimentation and physical reworking. Right panels show trait–biomass alluvial diagrams for representative low-LV stations, highlighting low invertebrate biomass, dominance of infaunal deposit feeders, limited epifaunal suspension feeders, and low functional diversity (trait roles).

3.4.2 Intermediate LV1: stable seafloor habitats with moderate advection

Stations with intermediate LV scores (*e.g.*, KOF3, DB2, ACF4) displayed intermediate benthic invertebrate biomass (KOF3 biomass = 2.75 g C m^{-2}, DB2 = 5.22 g C m^{-2} and ACF4 = 4.94 g C m^{-2}) with higher contributions from epifaunal functional groups than seen at stations with lower LV scores. Stations KOF3 and ACF4 showed highly comparable trait composition, with similar distributions across all trait categories, showing a convergence in functional structure despite being located in different coastal systems (Fig. 5). In contrast, ACF4 and DB2 were more similar in total benthic carbon biomass (approximately 5 g C m^{-2}), yet DB2 displayed a broader representation of functional roles, indicating a more functionally heterogeneous assemblage (Fig. 5). Both ACF4 and DB2 were relatively exposed to open-water influence (embayment setting in DB2; a near-shelf position in ACF4), representing increased connectivity to offshore waters, highlighting potentially stable but moderately advective bottom conditions where both SOC and suspended particles influence benthic resource availability.

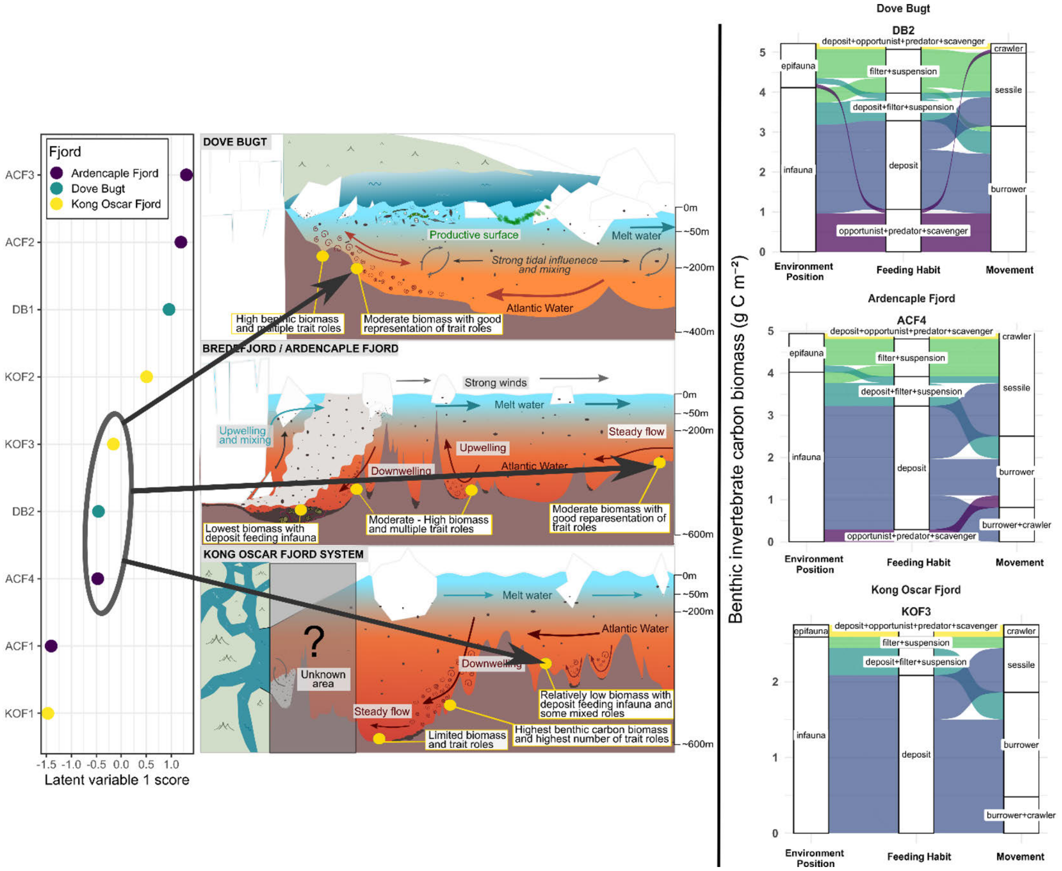

Figure 5 | Left panel shows stations with intermediate LV scores (highlighted) occupying the central portion of the latent gradient. Central panels present conceptual schematics representing relatively stable seafloor conditions with moderate bottom-water advection. Right panels display trait–biomass alluvial diagrams for representative intermediate-LV stations, illustrating increases in invertebrate biomass and functional diversity (trait roles), including epifaunal suspension-feeding and mixed strategies, compared with low-LV stations.

High LV scores: advective, hydrodynamically exposed stations.

Stations with high LV values (*e.g.*, DB1, ACF2-3, KOF2) supported the highest benthic biomass across all the stations (DB1 biomass = 8.01 g C m^{-2}, ACF2 & 3 = 4.80 and 5.80 g C m^{-2} and KOF2 = 11.6 g C m^{-2}; Fig. 6). The proportion of trait roles among the community was substantially higher than at low-LV stations, including epifaunal suspension feeders, mobile scavenger-predators, and species capable of mixed feeding strategies. Among these stations, KOF2 exhibited the highest total benthic biomass overall and the largest proportional contribution of suspension feeders. DB1 and ACF2 showed highly similar trait composition in terms of relative proportions across feeding and movement categories, although DB1 supported higher total biomass than ACF2. ACF3 displayed a trait composition comparable to DB1 and ACF2 but had the highest proportional representation of taxa capable of mixed feeding strategies, resulting in the most even distribution of functional roles among the high-LV stations. These high-LV-scoring stations are located along the steepest bathymetric sills compared to the other stations.

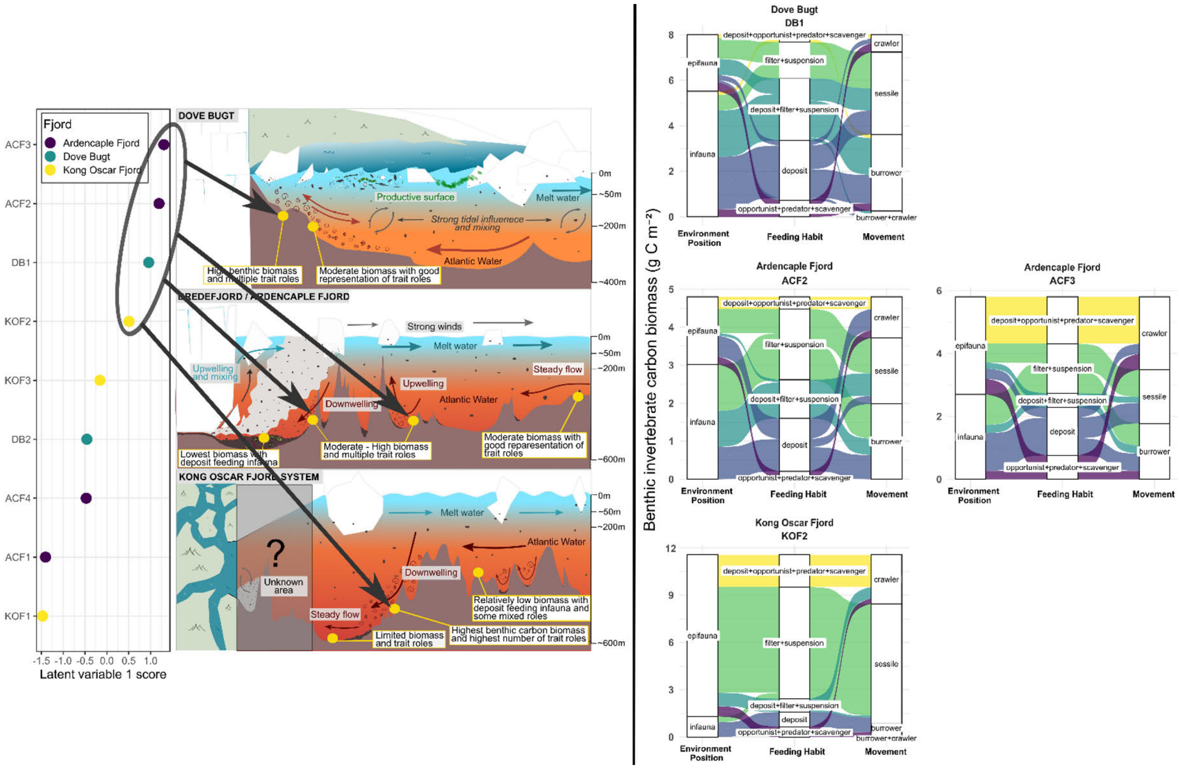

Figure 6 | Left panel shows stations with high LV scores (highlighted) occupying the positive end of the latent gradient. Central panels present conceptual schematics representing hydrodynamically exposed settings influenced by enhanced

advection, mixing, and lateral particle transport. Right panels display trait–biomass alluvial diagrams for representative high-LV stations, illustrating dominance of epifaunal suspension feeders and an increase in mixed feeding strategies, higher representation of crawling and sessile taxa, and elevated benthic invertebrate biomass and functional diversity relative to low-LV stations.

4. Discussion

Our results reveal a partial decoupling between vertical POC export, sedimentary organic carbon stocks, and their translation into benthic carbon biomass and community trait structure across Northeast Greenland coastal systems. Despite relatively similar bottom-water properties among systems, marked spatial variability in carbon accumulation, benthic biomass, and trait composition suggests that local environmental context influences how carbon is redistributed, retained, and utilised at the seafloor. In the following sections, we examine the role of AW connectivity and hydrographic structure, the relationship between vertical carbon export and sedimentary carbon accumulation, and how benthic traits and spatial context shape benthic biomass and functional diversity.

4.1 Hydrographic structuring and Atlantic Water influence

We found that the three high-latitude coastal systems exhibited similar bottom temperature, salinity, and oxygen profiles, which were representative of AW (Fig. 1). While AW influence might have been expected in the more open Kong Oscar Fjord system (Gjelstrup et al. 2022), and within the shallow, heavily tidally influenced basin of Dove Bugt (Zoller et al. 2023), its occurrence at the innermost stations of the connected Brede Fjord and Ardencaple Fjord system was unexpected. This was particularly notable given the presence of multiple shallow sills, in places rising to approximately 50 m depth, and the lack of prior documentation of AW in this system. This observation highlights that sill depth alone does not necessarily constrain hydrographic connectivity in these high-latitude glacial fjords, even on outflowing shelves (Bao and Moffat 2024). One plausible mechanism is the episodic drawdown of deeper waters associated with intense glacier calving and ice loss, which can induce compensatory inflow of offshore waters to replace displaced mass (Hill et al. 2017). Such events are often accompanied by enhanced mixing, partial reflux, and temporary weakening of stratification, facilitating intermittent deep-water renewal despite shallow sills (Bao and Moffat 2024). However, the frequency and persistence of such renewal events remain unknown, raising the possibility that inner fjord basins may alternate between periods of active flushing and longer phases of reduced ventilation (Benn et al. 2017), with implications for nutrient retention, sediment redox conditions, and the metabolic demands and functional organisation of benthic communities (Jordà-Molina et al. 2019).

Another important implication of this widespread AW presence is that the benthic environment may have been exposed to modified hydrographic conditions for longer than can be detected from snapshot sampling observations. Recent work indicates that AW has been shoaling along the Northeast Greenland shelf at rates of tens of metres per decade (Schaffer et al. 2017; Gjelstrup et al. 2022; Wekerle et al. 2024), suggesting that benthic communities, by their position at the seafloor, are likely among the first to experience the sustained change (Jordà-Molina et al. 2023; Bodur et al. 2024). The hydrographic homogeneity observed here indicates that AW influence serves as a consistent background condition, in contrast to the marked spatial differences in vertical carbon flux, sedimentary carbon stocks, and trait-based benthic composition. From this perspective, rather than single variables, such as temperature, which often remain as key and widely studied drivers of benthic processes (Kortsch et al. 2012; Ashton et al. 2017; Komendić et al. 2024; Sen et al. 2024), benthos are mediated through interactions with food availability, energy supply, and sedimentary conditions, which covary with hydrography and carbon pathways in these systems (Armitage et al. 2024), as seen in this study's multiple correlations in environmental parameters (SM, Fig. S2). Therefore, it is inferred that the observed biological patterns of biomass and traits in this study are driven by resource landscapes rather than water-mass characteristics, although we recognise that this inference is based on spatial contrasts across three coastal systems rather than temporal dynamics, which may overlook impacts to species assemblages and function related to AW.

4.2 (De-) Coupling of hydrography, vertical carbon export, and sedimentary carbon

The estimated attenuation in POC export between the deepest sediment traps and the seafloor was comparatively small relative to the stronger attenuation observed higher in the water column. The upper water column is where vertical carbon export is shaped by the interaction of spatial variability in surface primary production with physical (e.g. bottom currents, resuspension, and lateral particle transport) and biological processes (e.g. zooplankton grazing and remineralisation), which together regulate the efficiency with which organic matter is transferred to the benthos. Depth profiles consistently showed changes in flux attenuation at the transition between Surface and Polar Waters and Atlantic Water at ~100–200 m (Fig. 1 and 2), reflecting the strong vertical structuring characteristic of Northeast Greenland shelf systems (Gjelstrup et al. 2022). Such water-mass boundaries likely regulate particle transformation and transfer, constraining the efficiency with which surface-derived material is exported to depth. In addition to this physical control, biological and topographic processes further modify vertical carbon transfer. Complex bathymetry, including sills and troughs, promotes lateral and vertical redistribution of particles, integrating material from multiple sources before it reaches the seafloor (Piepenburg et al. 1997; Reigstad et al. 2008; Bao and Moffat 2024). At the same time, zooplankton communities are highly variable and spatially patchy, often forming dense swarms that exert strong control over particle transformation through grazing, remineralisation, and the repackaging into faecal pellets at localised depths, generating variability in attenuation and export efficiency (Estapa et al. 2021; Iversen 2023; Svensen et al. 2024). These processes weaken the link between surface production and the amount of carbon reaching the benthos.

Temporal variability further complicates the relationship between pelagic export and sedimentary carbon accumulation by separating the timescales over which these processes operate. In Arctic systems, carbon export is often dominated by episodic production pulses following sea-ice retreat and meltwater-induced stratification earlier in the productive season (Carmack et al. 2016; Niemi et al. 2024). Sediment trap deployments capture only these short-term flux dynamics and may therefore miss episodic high-flux events or alternative pathways such as active transport by vertically migrating organisms (Estapa et al., 2021; Iversen, 2023). In contrast, sedimentary carbon stocks integrate organic matter delivery over much longer timescales, from seasons to years or longer (Iversen 2023), and thus retain signals of earlier export events not resolved by snapshot measurements. As sampling in this study occurred toward the end of the productive season, measured fluxes either reflect residual export following earlier bloom-driven peaks associated with sea-ice retreat or a later regenerated summer production, while sedimentary carbon stocks may still integrate either of these inputs. Consistent with this temporal mismatch, our data show a decoupling between carbon flux and sediment stocks. Sedimentary carbon exhibited pronounced spatial variability that did not align directly with estimated POC export to the seafloor: stations with high SOC (e.g. ACF3–ACF4 and KOF1) were not associated with the highest POC measurements, whereas stations with relatively higher exported POC (e.g. DB1) did not exhibit proportionally elevated SOC. Similar decoupling between pelagic flux and benthic carbon storage has been reported in Arctic systems (Wiedmann et al. 2020; Bodur et al. 2024), further indicating that sedimentary carbon stocks reflect the cumulative effects of episodic and spatially patchy export, rather than instantaneous flux, with hydrographic structure, biological processing, and local depositional conditions regulating the delivery and retention of organic matter at the seafloor.

4.3 Carbon supply pathways and trait-mediated benthic carbon biomass

While the above section outlines how the vertical POC flux and sedimentary organic carbon define the potential resource landscape at the seafloor, the Generalised Linear Latent Variable Model results suggest that the incorporation of carbon into benthic invertebrate biomass depends less on bulk carbon availability itself than on how different functional strategies access and utilise available resources. Filter and suspension feeding taxa exhibited the strongest and most consistent positive relationships with POC flux, sedimentary organic carbon, and their interaction, yet were restricted to a subset of stations (KOF2, DB1, ACF2, ACF3) spanning variable carbon environments. Their response to the interaction term suggests that neither flux nor SOC alone is sufficient, but that sustained coupling between pelagic inputs and benthic sediments is required to support high standing biomass. The persistence of these often long-lived, immobile Arctic taxa likely depends on carbon availability extending beyond sporadic pulses, through longer-term retention, redistribution, or background suspended supply, as well as resource quality and nutrient composition (Yool et al. 2017; Gunnvør et al. 2018). In contrast, several prominent infaunal trait groups, including deposit feeders, burrowers, and mixed deposit–filter feeders, showed little or no statistical response to bulk carbon predictors, with coefficients centred near zero. Rather than indicating insensitivity to organic matter, this suggests that these strategies depend on resource characteristics not captured by bulk carbon metrics, such as particle size, lability, and biochemical composition. Across both epifaunal and infaunal pathways, resource quality therefore emerges as a key constraint, with biochemical components such as lipids, frequently utilised as energy storage strategies in Arctic taxa, supporting reproduction and persistence through prolonged low-input periods (Clarke 1983; Bridier et al. 2023; Cautain et al. 2024). Consistent with this, benthic consumers may preferentially assimilate sea-ice-derived organic matter over pelagic sources even when total carbon availability is similar, reflecting differences in energetic value rather than quantity alone (Cautain et al., 2022; Clarke, 1983; Niemi et al., 2024; Yunda-Guarin et al., 2020). Together, these contrasting responses indicate that benthic biomass is governed not simply by carbon supply, but by the interaction between supply pathways and resource quality, with different trait strategies exploiting distinct components of the carbon pool that are not equally captured by bulk flux or sedimentary measures.

Mixed feeding strategies provide further insight into how carbon supply is redistributed within the benthic assemblage. The proportion of mixed feeding strategists (i.e., those that are jointly deposit feeders, predators, and scavengers) increased along the high-LV end of the gradient, especially at KOF2 and ACF3, where benthic biomass was also relatively the highest (SM, Fig. S1). This shift coincided with a greater contribution of epifaunal suspension feeders, linked to carbon flux and sedimentary carbon, indicating enhanced benthic secondary production within these assemblages. Rather than reflecting reliance on a single prey source, the increased representation of mixed strategists suggests exploitation of advected particulate matter, sedimentary detritus, and benthic secondary production biomass (*e.g.*, increased biomass of sessile filter feeders). In such biomass-rich systems, trophic flexibility may allow organisms to exploit spatially and temporally variable resources across co-occurring energy pathways (McMeans et al. 2015; Mavraki et al. 2020). Trophic generalism, however, is not necessarily advantageous. The energetic and morphological trade-offs associated with flexibility may constrain its persistence under carbon-limited conditions, where specialised deposit or suspension feeders are better optimised for dominant resource pools (Bridier et al. 2021b; Yunda-Guarin et al. 2022, 2023). Yet, at high biomass stations characterised by elevated benthic secondary production and increased functional and structural complexity, mixed feeding strategies become more prominent and may have an advantage during periods of low carbon input. Therefore, these assemblages appear not only productive but functionally integrated, with multiple feeding modes operating simultaneously to process and redistribute carbon, reinforcing benthic biomass accumulation through interconnected energy pathways.

4.4 A hydrodynamic gradient potentially structures benthic carbon biomass and functional diversity

Since the latent-variable modelling approach captures residual ecological structure not explained by measured predictors, it can reveal underlying processes shaping benthic communities that are not directly resolved by conventional environmental measurements. Our latent variable analysis suggests that, beyond vertical carbon flux and sedimentary carbon stocks, benthic carbon biomass and functional composition are structured by an additional ecological gradient. Although no single measured environmental variable explained the latent variable, its structure became clearer when LV station scores were examined within their bathymetric setting and alongside benthic trait composition and biomass (Figs. 4-6). In this spatial context, LV scores clustered along gradients of basin exposure, suggesting that the LV captures an emergent hydrodynamic regime rather than a missing discrete predictor. This regime likely reflects the cumulative effects of horizontal advection, sill-driven transport, tidal mixing, and resuspension processes that redistribute carbon across fjord basins but remain poorly represented by static hydrographic or sedimentary metrics.

Patterns of benthic invertebrate hotspots (*e.g.*, elevated species richness, abundance, and biomass) are widely documented on seamounts, submarine canyons, ridges, and shelf breaks, where topographic complexity intensifies near-bed currents, which enhance particle delivery and promote both benthic and fish assemblages (Clark et al. 2010; Rowden et al. 2010; Boehlert and Genin 2013). These hydrodynamically exposed environments often favour epifaunal filter feeders such as sponges, corals, and other suspension feeders, which benefit from increased encounter rates with suspended particles and reduced sediment clogging (Lundsten et al. 2009; Rowden et al. 2010). Through their high filtration capacity, these communities capture and transform organic matter into benthic secondary production, generating localised secondary production hotspots that support mobile scavengers and predators and give rise to functionally diverse benthic food webs sustained by horizontal advection rather than vertical export alone.

We hypothesise that a similar configuration likely emerged in our coastal systems, with high latent-variable scores situated on steep sills supporting the highest benthic invertebrate biomass and the most diverse, functionally rich assemblages, even in the absence of elevated POC export or SOC. Furthermore, high-LV stations supported epifaunal suspension feeders alongside a broader representation of functional groups, including mixed feeding strategists, indicating enhanced secondary production and greater redistribution of carbon across co-occurring feeding modes under advective conditions. These stations therefore indicate advective settings in which bathymetric orientation and sill-mediated circulation enhance particle supply, facilitating the coexistence of multiple feeding modes and trophic interactions, as seen with Boehlert & Genin (2013) and Rowden et al. (2010). Parallel to this, Barnes & Sands (2017) also show how benthic communities increase in biomass and in the number of functional groups in response to enhanced carbon accumulation via even finer hydrographic scales, such as environments with boulder fields and mixed hard–soft interfaces, highlighting the importance of considering local-scale hydrodynamic context when interpreting benthic–pelagic coupling and carbon pathways in glacial coastal systems. Further illustrating this point is station ACF1 in the Ardencaple Fjord system, which has a low latent variable score and is located close to the marine-terminating glacier. This station lies within a zone of elevated turbidity and sediment input, and its landward position relative to a shallow sill approximately 40 km from the glacier likely promotes the trapping of fine material, favouring depositional conditions and disturbance-tolerant infaunal communities. Recognising hydrodynamically driven habitat heterogeneity as a fundamental driver of benthic structure therefore provides a more mechanistic framework for predicting ecosystem responses to both climatic and anthropogenic change in Arctic coastal systems.

5. Implications and future perspectives on high-latitude benthic carbon storage

The findings of this cross-disciplinary study demonstrate that benthic communities in Northeast Greenland coastal systems are shaped by a hierarchy of processes: (1) regional carbon production and export, (2) local seafloor-sediment carbon availability, and (3) hydrodynamic redistribution that interacts with slope and aspect. As climate-driven changes in meltwater discharge, glacier retreat and AW inflow intensify, the balance between vertical export, horizontal transport and local retention is likely already shifting with changes that will modify both the magnitude and functional composition of benthic carbon stocks. Most studies of marine carbon cycling, particularly in polar systems, focus almost exclusively on vertical carbon flux as the primary pathway linking ocean productivity to benthic carbon storage (Snelgrove et al. 2018; Wiedmann et al. 2020; März et al. 2022). This emphasis has shaped both empirical approaches and conceptual models, yet our results show that a snapshot of vertical carbon export alone provides an incomplete view of the seafloor carbon environment over longer time scales.

Horizontal and sill-driven transport processes redistribute organic matter across heterogeneous basins in ways that can amplify, dilute or completely decouple vertical POC flux from benthic carbon supply (Barnes and Sands 2017; Yin et al. 2024). These lateral pathways are rarely measured directly and remain largely absent from carbon budgets. In the context of accelerating Arctic change, where meltwater discharge, glacier retreat and shifts in water-mass inflow are reshaping fjord circulation, incorporating these horizontal processes is essential for understanding how carbon is transferred, transformed and retained in benthic communities. Our results highlight the limitations of linking short-term vertical carbon export directly to benthic food supply and instead emphasise the importance of integrating carbon export, sediment geochemistry, hydrodynamics, and trait structure to understand carbon transfer and retention at the seafloor and benthos' potential role in nature-based climate mitigation strategies.

6. Conclusions

This study demonstrates that, despite broadly homogeneous bottom-water conditions, benthic communities exhibited pronounced spatial heterogeneity, driven by interactions among vertical carbon export, sedimentary carbon stocks, and hydrodynamic processes that regulate carbon delivery and retention. Trait-based responses further show that benthic carbon biomass is not governed simply by the presence of organic carbon, but by trait-mediated access to distinct carbon pathways and trophic positions within the benthic food web. Only a subset of trait strategies translated the vertical POC flux or sedimentary organic carbon into standing biomass, highlighting the importance of carbon quality, trophic mediation, and access pathways rather than bulk carbon quantity alone.

By identifying a latent hydrodynamic gradient that structures benthic biomass independently of traditional predictors, this work emphasises the critical role of horizontal transport and sill-driven circulation in Arctic coastal systems. Together, these findings call for a shift beyond vertically focused carbon frameworks toward integrated, multi-scale perspectives that explicitly link physical circulation, carbon redistribution, and benthic functional ecology when assessing the resilience and carbon storage potential of Arctic coastal systems under rapid environmental change. Further progress will require process-oriented approaches to resolve the interacting physical, biological, and ecological controls on carbon delivery and utilisation at the seafloor.

Code and data availability

The datasets and R scripts supporting the findings of this study have been deposited in a FAIR-aligned public repository [e.g. Zenodo / PANGAEA]. During the review process, access is restricted to reviewers via the Copernicus system. Upon acceptance of the manuscript, all data and code will be made publicly available and assigned a permanent DOI. The repository includes all metadata necessary to reproduce the analyses and figures presented here. Environmental and sediment trap data used in this study were originally published by Wiedmann and Svensen (2024) and are available via their respective repository.

Supplement link

The link to the supplement will be included by Copernicus.

Author contributions

PA, AT and CS collected the data. PA, CS, BO, JL, and MWK curated the data. PA performed the formal analysis and visualisation. PA, AT, and MCN conceptualised the study and developed the methodology. PA prepared the original draft of the manuscript. All authors (PA, MCN, CS, BO, JL, MWK, and AT) contributed to reviewing and editing the manuscript. AT and CS acquired the funding.

Competing interests

The authors declare that they have no competing interests.

Disclaimer

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Review statement

The review statement will be added by Copernicus Publications listing the handling editor as well as all contributing referees according to their status anonymous or identified.

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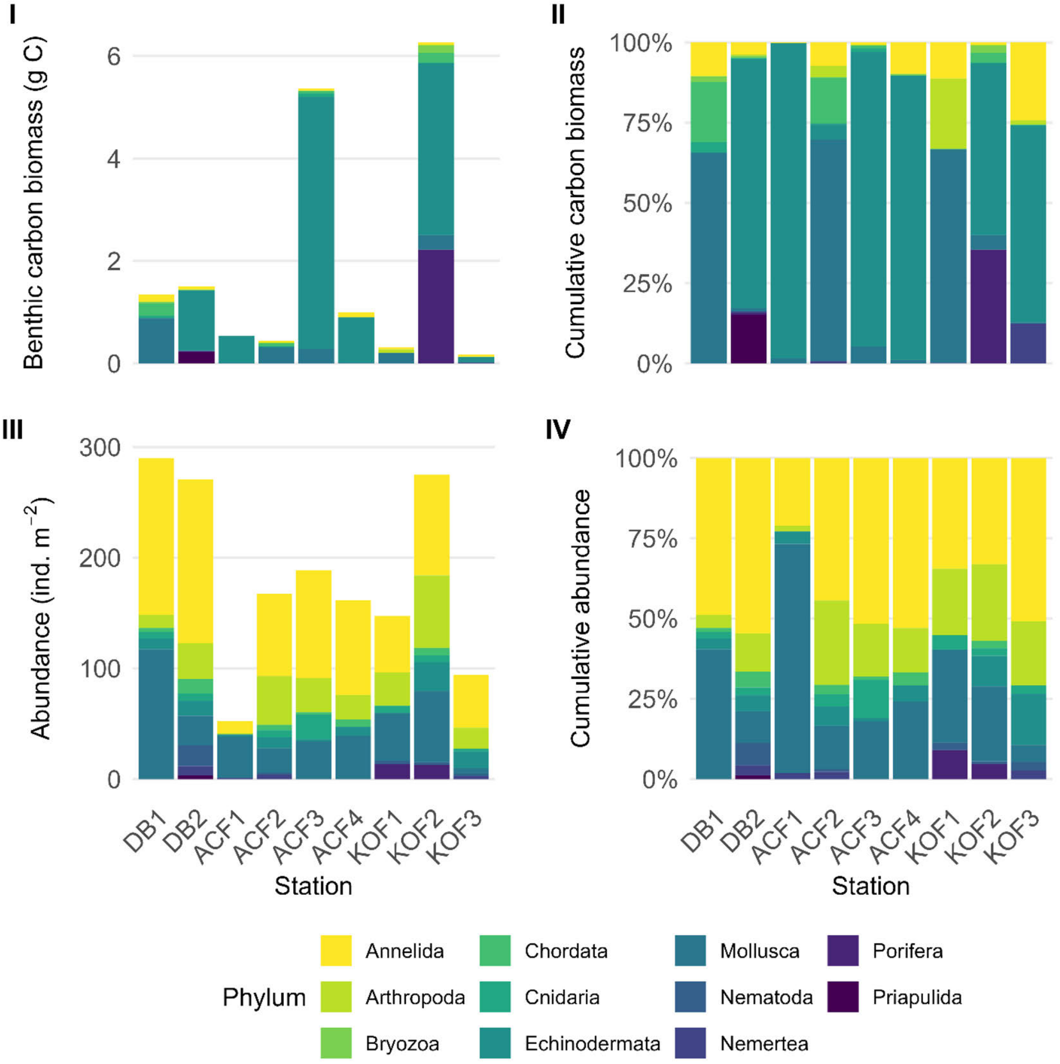
Supplementary Material

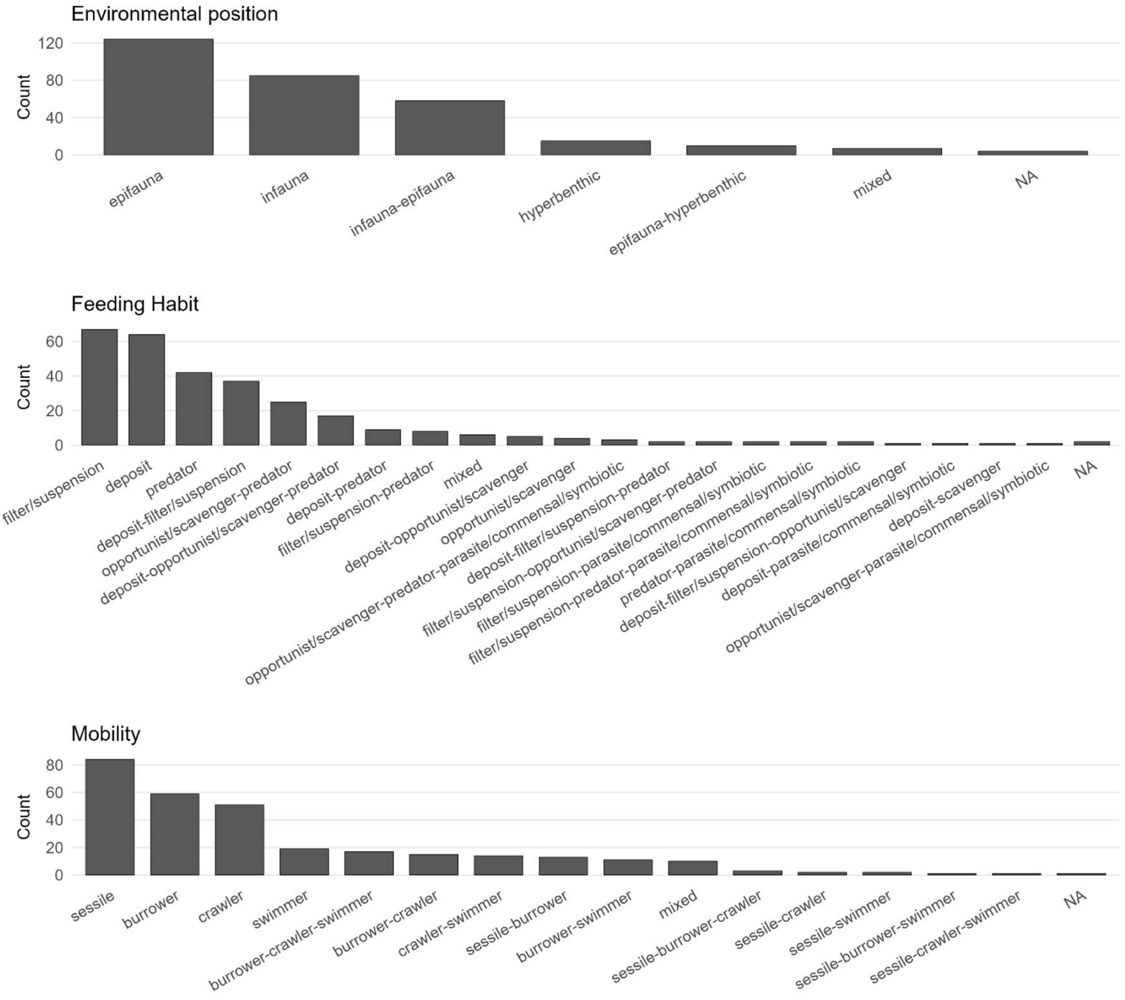
Species Biomass & Composition

Figure S1. Taxonomic composition of benthic communities across sampling stations in Northeast Greenland coastal systems. Panels (I) and (II) show absolute and cumulative benthic carbon biomass (g C), respectively, while panels (III) and (IV) show absolute and cumulative abundance (ind. m^{-2}). Absolute values are shown as stacked bars partitioned by phylum, and cumulative panels display proportional contributions of each phylum to total community biomass or abundance. Colours indicate major benthic phyla. Stations are ordered by coastal system and inner–outer position within each system; Dove Bugt (DB), Ardencaple Fjord (ACF), and Kong Oscar Fjord (KOF).



Traits

Figure S2. Distribution of categorical trait assignments across all taxa in the full benthic community prior to truncation at 95 per cent cumulative biomass. Shown are counts of species for three traits: environmental position, feeding habit, and mobility. Bars represent the number of species assigned to each trait category. Categories comprise multiple terms from fuzzy-coded trait assignments that were subsequently translated into composite text labels, such that species with any affinity to multiple modalities (*e.g.*, deposit feeder and predator) are represented as combined categories (*e.g.*, deposit-predator). NA denotes species for which trait information was unavailable.



Environmental Variables

Figure S3. Relative grain size composition across transects. Stacked bars show the percentage contribution of mud, silt, sand, and gravel to surface sediment composition at each transect. Percentages sum to 100 per cent for each transect.

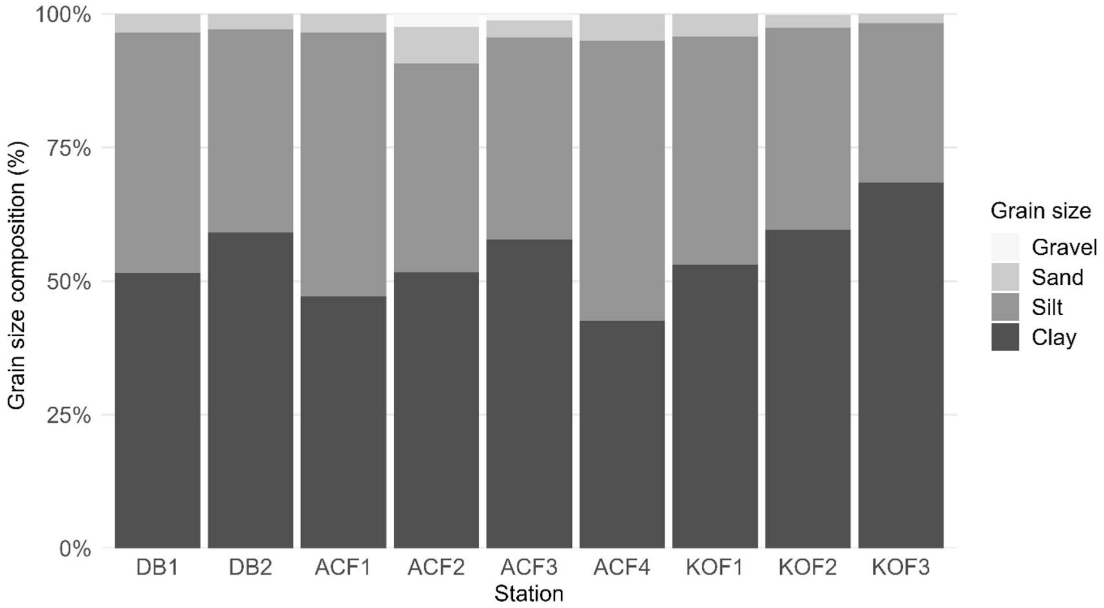
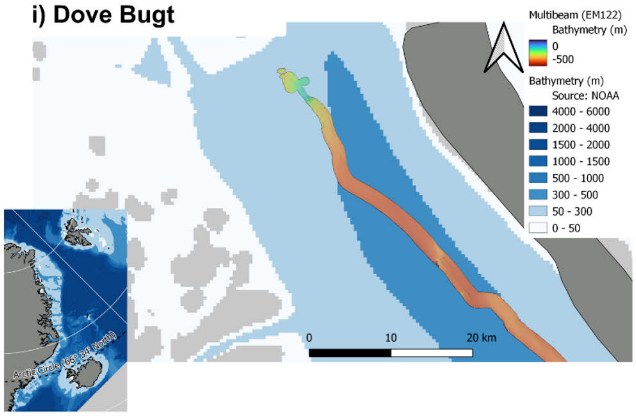
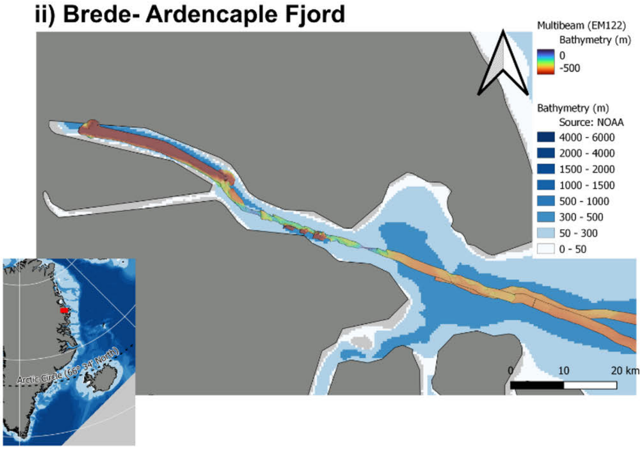


Figure S4. Multibeam bathymetry of three Northeast Greenland coastal systems: (i) Dove Bugt, (ii) Brede–Ardencaple Fjord, and (iii) Kong Oscar Fjord. High-resolution multibeam data (EM122) are shown as a colour overlay representing depth in metres, enhanced by hillshade. Background bathymetry is derived from NOAA and displayed in depth intervals (m). Grey areas represent land. Insets indicate the regional location of each coastal system within Northeast Greenland. Scale bars are shown in kilometres.

i) Dove Bugt



ii) Brede- Ardencaple Fjord



iii) Kong Oscar Fjord

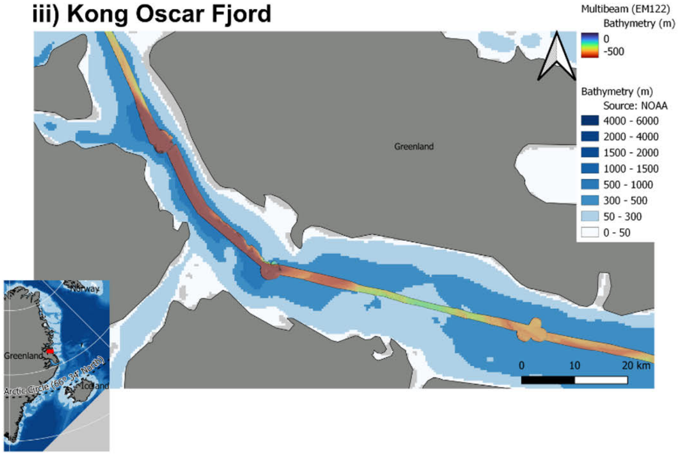


Figure S5: Violin plots show the environmental variation across coastal systems in Northeast Greenland based on raw values. Mud, silt, sand, gravel are grain-size fractions that sum together to 100% and aspect and slope are seabed topographic variables. Black points indicate individual station values, with violins illustrating the distribution within each coastal system.

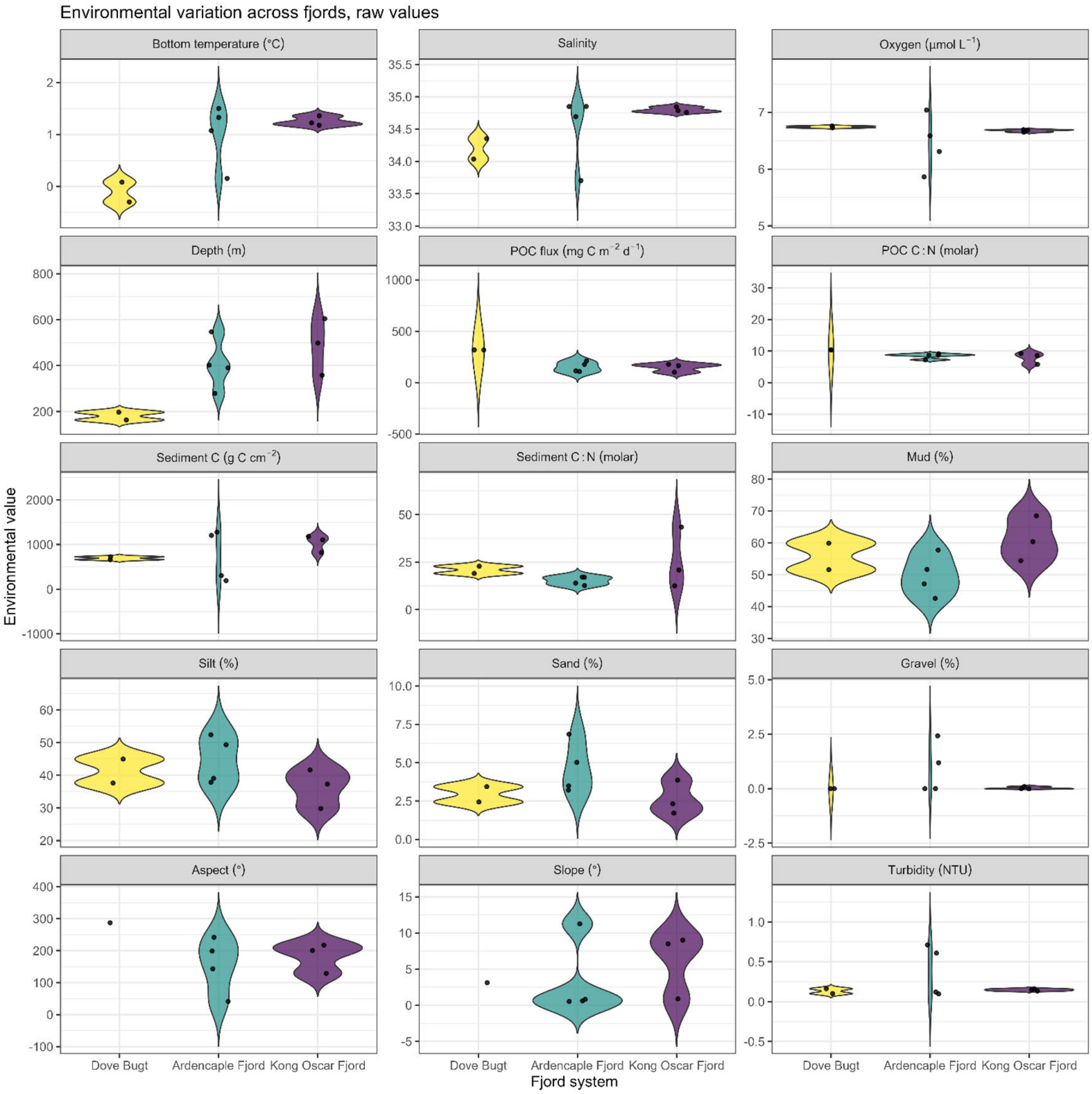
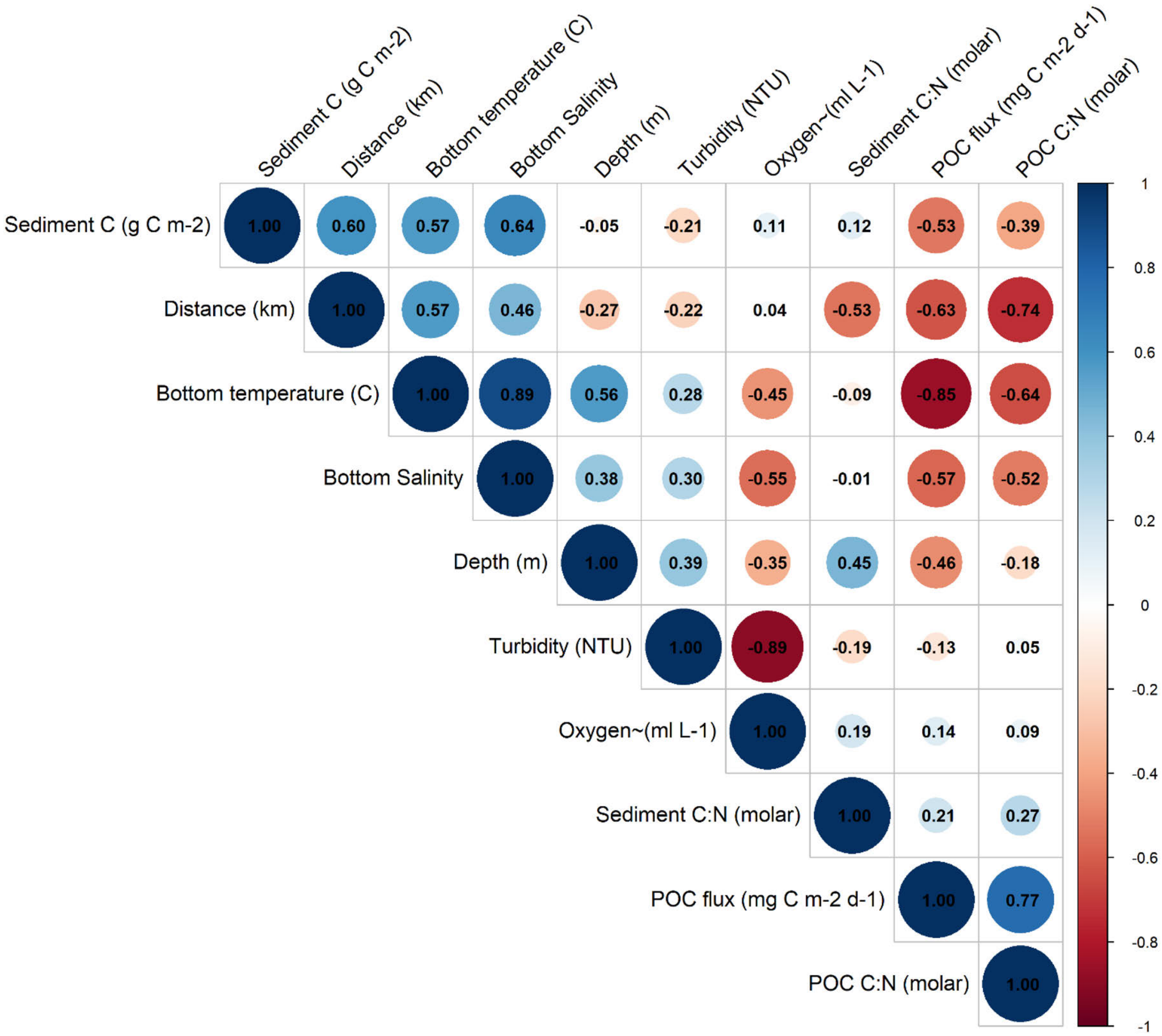


Table S6. Descriptive statistics for environmental variables measured across sampling stations in Northeast Greenland. For each parameter, the mean, standard deviation, and coefficient of variation (CV) are reported based on station-level values. CV is used as a relative measure of variability to facilitate comparison among variables with different units and ranges. Variability classes followed conventional thresholds: <5 % indicated very low variability, 5–20 % low, 20–50 % moderate, 50–90 % high, and >90 % extremely high. Several hydrographic variables exhibit low relative variability across stations, whereas carbon-related variables show moderate variability, and fluorescence and turbidity display high CV values driven by small absolute magnitudes rather than large absolute ranges.

Parameter	Mean	Std Dev	CV (%)	Interpretation
Depth	382	151.58	39.70%	Moderate variability
Temperature	0.8438	0.6716	79.60%	High variability
Salinity	34.5419	0.4188	1.21%	Very low variability
Oxygen	6.5924	0.3323	5.04%	Low variability
Fluorescence	0.0343	0.0314	91.50%	Extremely high variability
Turbidity	0.2494	0.2356	94.50%	Extremely high variability
Sediment Carbon	7.3345	3.5065	47.81%	Moderate variability
Sediment CN ratio	19.9305	9.4986	47.66%	Moderate variability
Flux POC	181.2273	71.6113	39.51%	Moderate variability
Flux CN ratio	8.6593	1.3928	16.08%	Low variability

Figure S7. Pairwise correlations among environmental variables measured across all stations in the three Northeast Greenland coastal systems. Circles represent Pearson correlation coefficients (r), with colour indicating the direction (blue positive, red negative) and size reflecting the strength of the correlation. Values are shown within each cell. Strong covariation among several hydrographic and carbon-related variables highlights substantial multicollinearity within the environmental dataset (see Methods).



GLLVM Model diagnostics and details

Figure S8. Frequency distributions of benthic trait biomass values included in the Generalised Linear Latent Variable Models (GLLVMs). Histograms show the distribution of biomass across individual trait categories, highlighting strong right skew, continuous positive values, and the presence of zeros across traits. These characteristics justify the use of the Tweedie distribution, which accommodates zero-inflated, right-skewed continuous data typical of benthic biomass measurements.

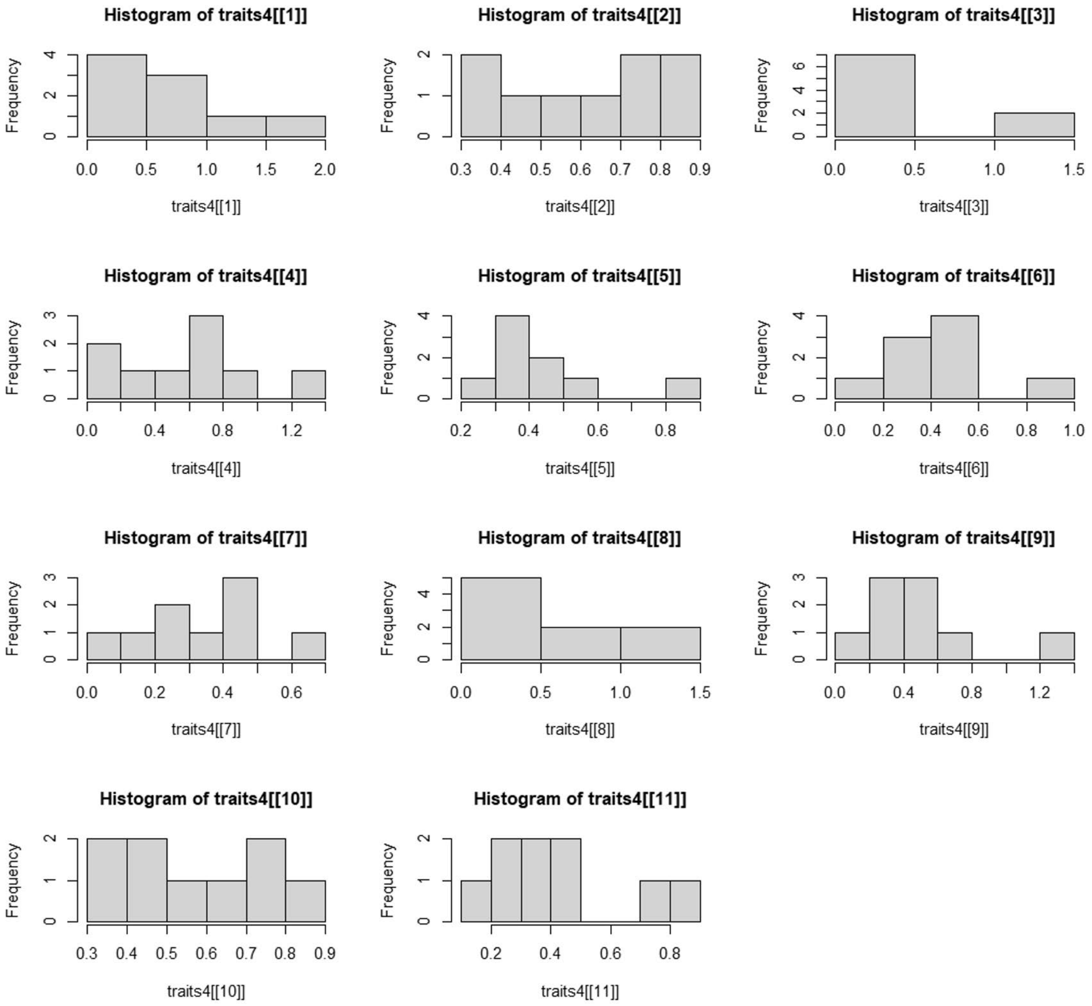


Figure S9: Diagnostic residual plots for the selected Generalised Latent Variable Model (GLLVM) with one latent variable. Panels show Dunn–Smyth residuals plotted against (i) linear predictors, (ii) theoretical quantiles (normal Q–Q plot), (iii) site index (rows), and (iv) trait biomass matrix index (columns), as well as (v) scale–location residual patterns. The final panel (vi) shows the single latent variable (LV1) ordered by sampling station (rather than LV1 score as shown in main text). Residuals show no major violations of model assumptions, with approximately constant variance, no strong trends against predictors or station/trait biomass, and acceptable normality of transformed residuals, indicating adequate model fit.

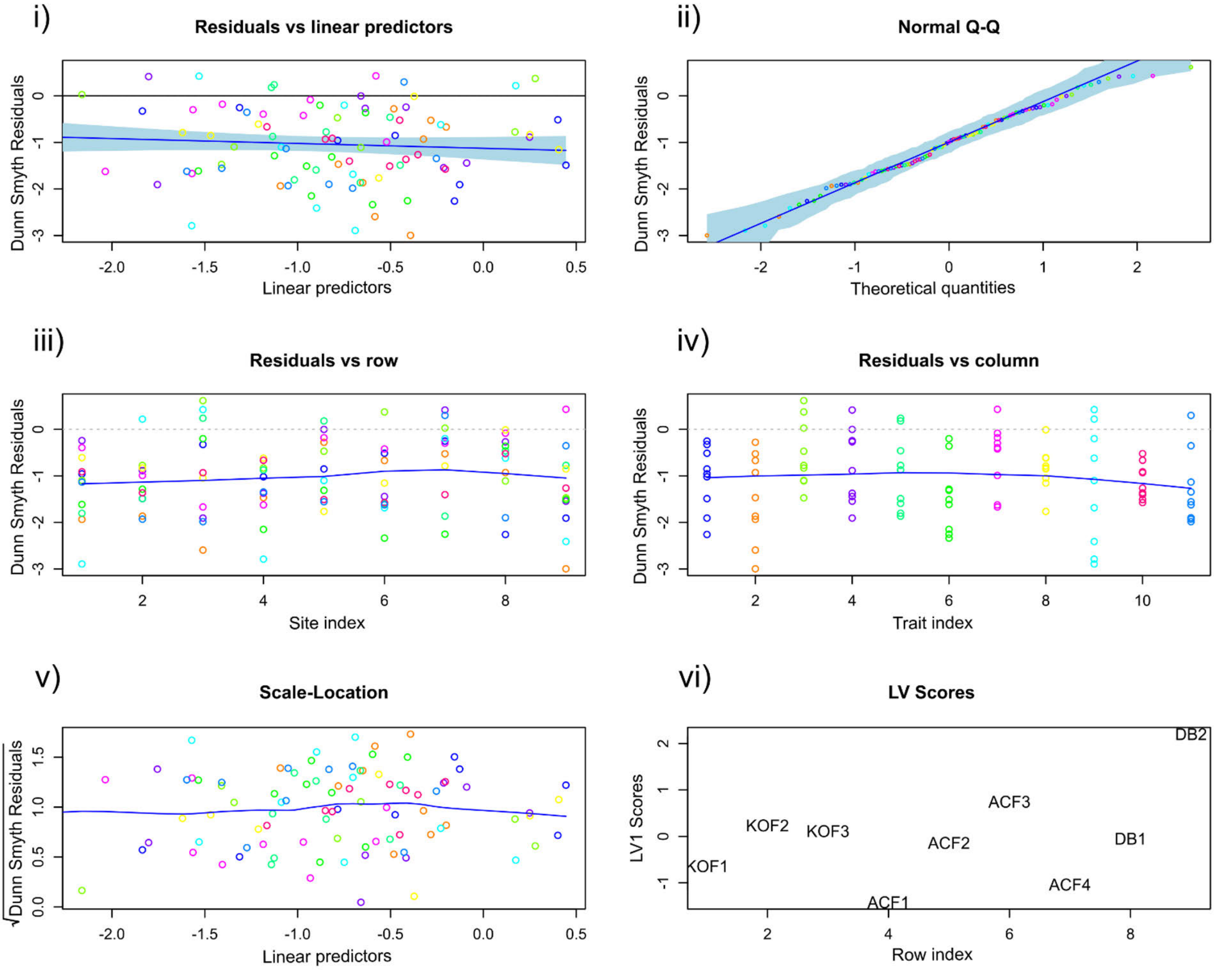


Table S10i. Akaike Information Criterion (AIC) values for Generalised Latent Variable Models (GLLVMs) fitted with zero to three latent variables. Grey text indicates models that did not converge reliably (2 and 3 latent variables). Although AIC decreases with additional latent variables, only the model with one latent variable represents a valid improvement in fit and is therefore selected as the best-supported model.

Latent variables	**df**	**AIC**	**BIC**	**Convergence**	**LogLik**
0	55	99.60582	242.3374	Yes	5.197
1	66	12.92206	184.2000	Yes	59.539
2	76	-26.45624	170.7729	No	89.228
3	85	-54.87447	165.7107	No	89.228

Table S10ii. Latent variable variances (σ²) for Tweedie gllvm models fitted with 0–3 latent variables. Variances near zero indicate unused or non-informative latent axes. While some model latent variable scores may provide the higher values, they are not meaningful if the models do not converge.

Model (k LVs)	**LV1**	**LV2**	**LV3**
0	–	–	–
1	0.835	–	–
2	0.864	0.068	–
3	0.740	0.263	0.046

Table S10iii. Model selection results for Generalised Latent Variable Models (GLLVMs) fitted with two latent variables, with and without system-level random effects. The null model (no latent variables, no random effects) is shown for reference. Random effects represent system-specific deviations (Ardencaple Fjord, Dove Bugt, and Kong Oscar Fjord). For each model, AIC, BIC, convergence status, and log-likelihood (with effective degrees of freedom) are reported. Random effects are small in magnitude, and the model without random effects provides the lowest AIC and similar log-likelihood, indicating no substantial improvement in model fit when including system-level random variation.

Latent variables	**Random effect**	**Size of random effects**	**AIC**	**BIC**	**Convergence**	**LogLik**
Null	N	-	15.555	101.194	Yes	25.223 (df=33)
2	Y	DB: 5.19e-05 ACF: 8.87e-06 KOF: -7.45e-05	14.948	188.820	Yes	59.526 (df=67)
2	N	-	12.922	184.200	Yes	59.539 (df=66)

Attenuation Coefficient

Figure S11i. Depth-dependent attenuation of particulate organic carbon (POC) flux at individual sampling stations across Northeast Greenland coastal systems. Panels show log-transformed POC flux (logPOC) plotted against log-transformed water depth (logDepth) for each station (KOF1–3, ACF1–3, DB1). Black points represent measured sediment trap fluxes at discrete depths, and blue lines indicate station-specific linear fits describing depth-related attenuation. Red dashed vertical lines mark the approximate depth of the deepest sediment trap used to estimate predicted POC flux reaching the seafloor. Slopes differ among stations, illustrating variability in the rate of POC attenuation with depth across coastal systems and along inner–outer gradients.

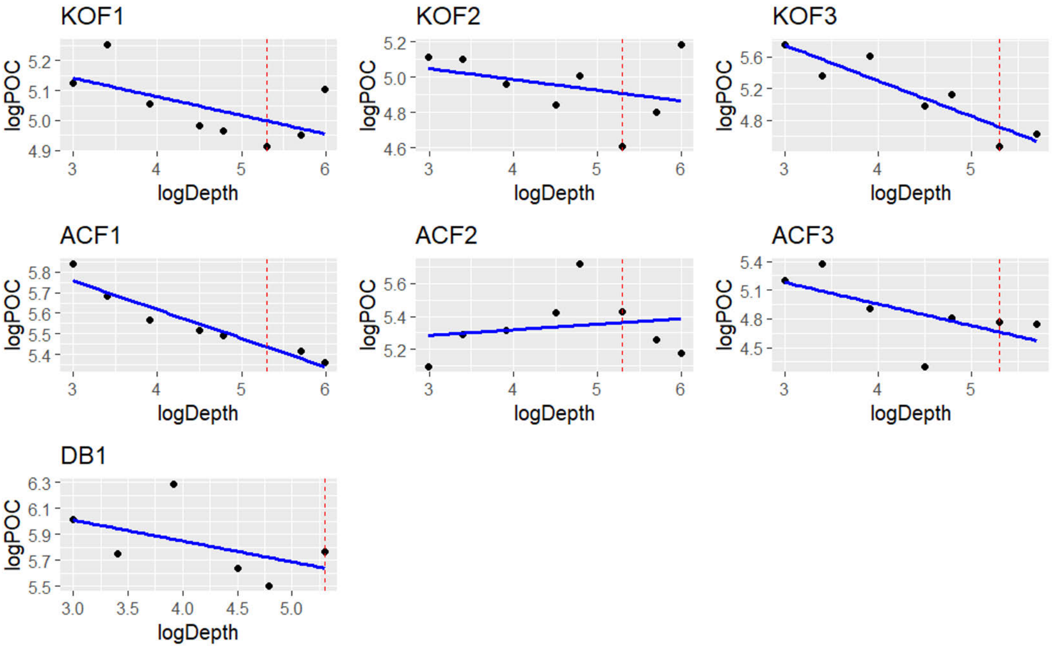


Table S11ii. Station-specific attenuation coefficients (b), deepest sediment trap depths and corresponding measured POC fluxes, seafloor depths, and estimated POC flux at the seafloor calculated relative to the deepest measured trap.

Transect	Attenuation slope (b)	Deepest trap depth (m)	Deepest trap POC (mg C m^{-2} d^{-1})	Seafloor depth (m)	Predicted seafloor POC (mg C m^{-2} d^{-1})
KOF3	-0.447	300	102	358	94
ACF3	-0.225	300	115	390	108
ACF1	-0.139	400	212	547	203
KOF1	-0.062	400	165	604	161
KOF2	-0.061	400	179	498	177
ACF2	0.034	400	177	402	177
DB1	-0.161	200	318	163	329

Figure S12. Spatial variation in surface sediment carbon–nitrogen (C:N) ratios across Northeast Greenland coastal systems. Boxes represent the interquartile range with median values indicated, and whiskers denote the data range. Horizontal dashed lines indicate approximate reference ranges commonly associated with relatively low, intermediate, and high C:N values for marine sediments, shown here for visual context only. No isotopic or source-specific analyses were conducted, and C:N ratios are interpreted descriptively as an index of spatial variability in sediment organic matter composition rather than as a definitive indicator of carbon source.

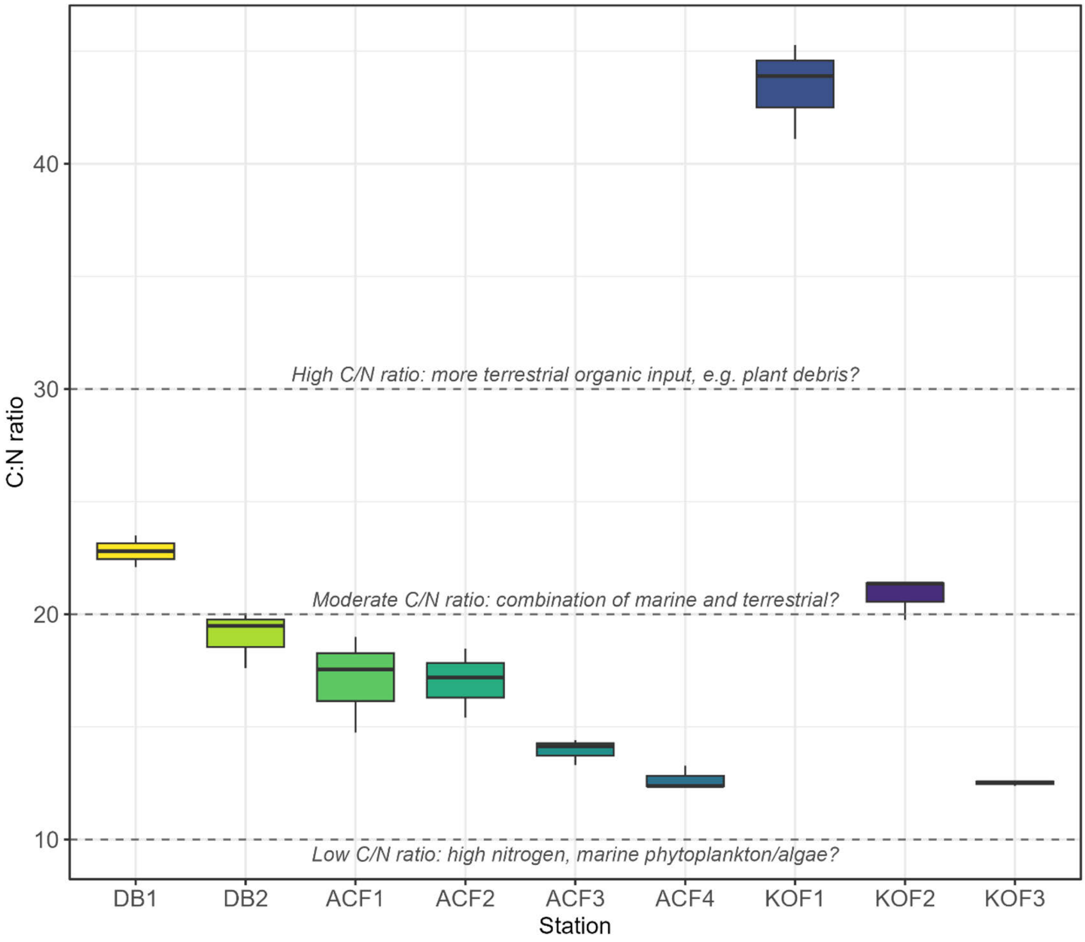
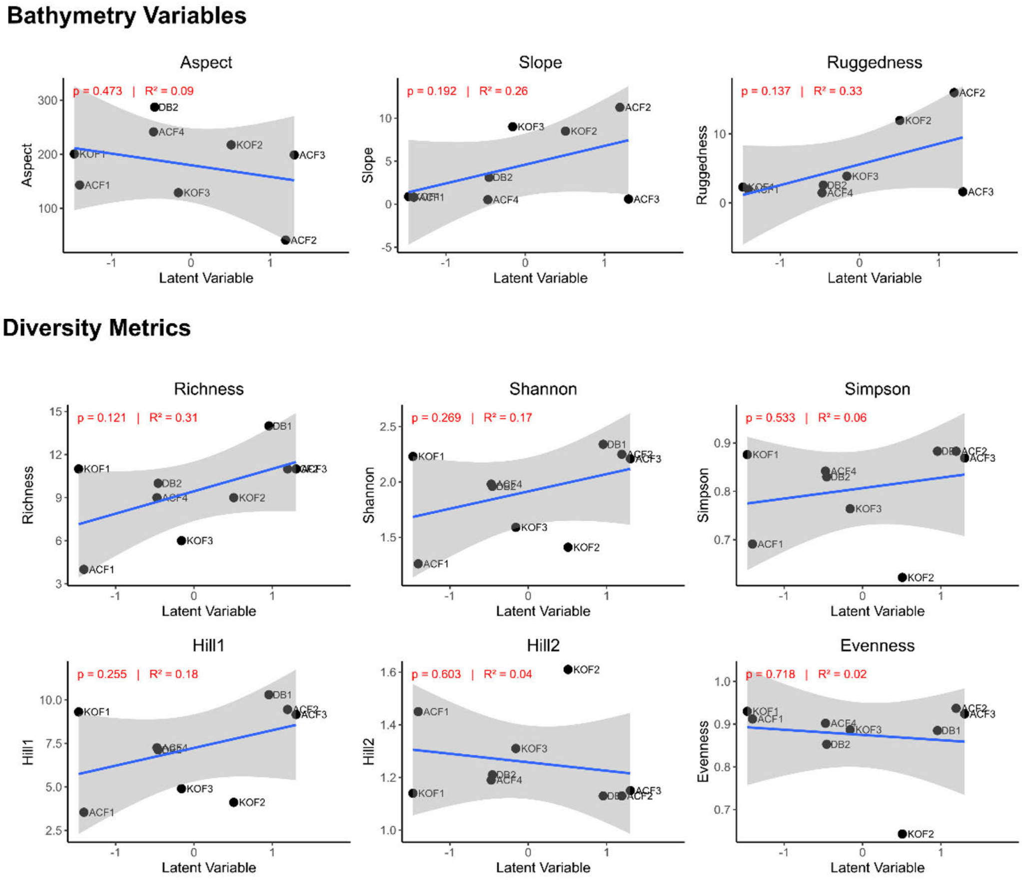


Figure S13. Potential linear relationships between latent variable and station-level functional diversity metrics (Richness, Shannon, Simpson, Hill1, Hill2, Evenness), environmental variables (water depth, CN flux, sediment CN ratio, dissolved oxygen, temperature, salinity, turbidity, and transect distance (inner – outer), and bathymetric terrain variables (aspect, slope, ruggedness). Each point represents a sampling station, labelled by station code. Lines show fitted linear regressions with 95% confidence intervals. Red text reports the p-value and coefficient of determination (R^2) for each model. Although none of the relationships are statistically significant, the panels illustrate the relative direction and magnitude of associations between the latent variable and diverse ecological and abiotic gradients, which may be useful for future study.



Environmental Variables

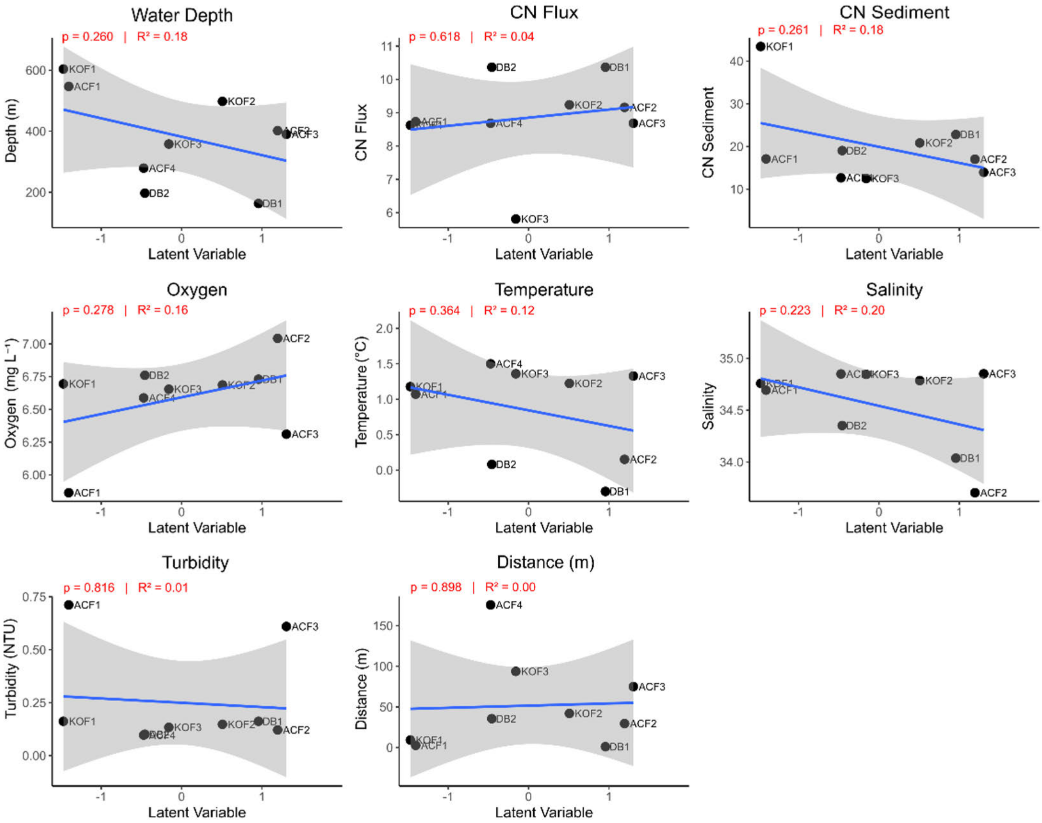


Figure S14. Conceptual schematic of hydrodynamic regimes, meltwater influence, and Atlantic Water inflow structure vertical mixing and carbon delivery pathways, shaping spatial patterns of benthic biomass and trait representation. Depth ranges are approximate and illustrate the typical hydrographic structure of Northeast Greenland coastal systems.

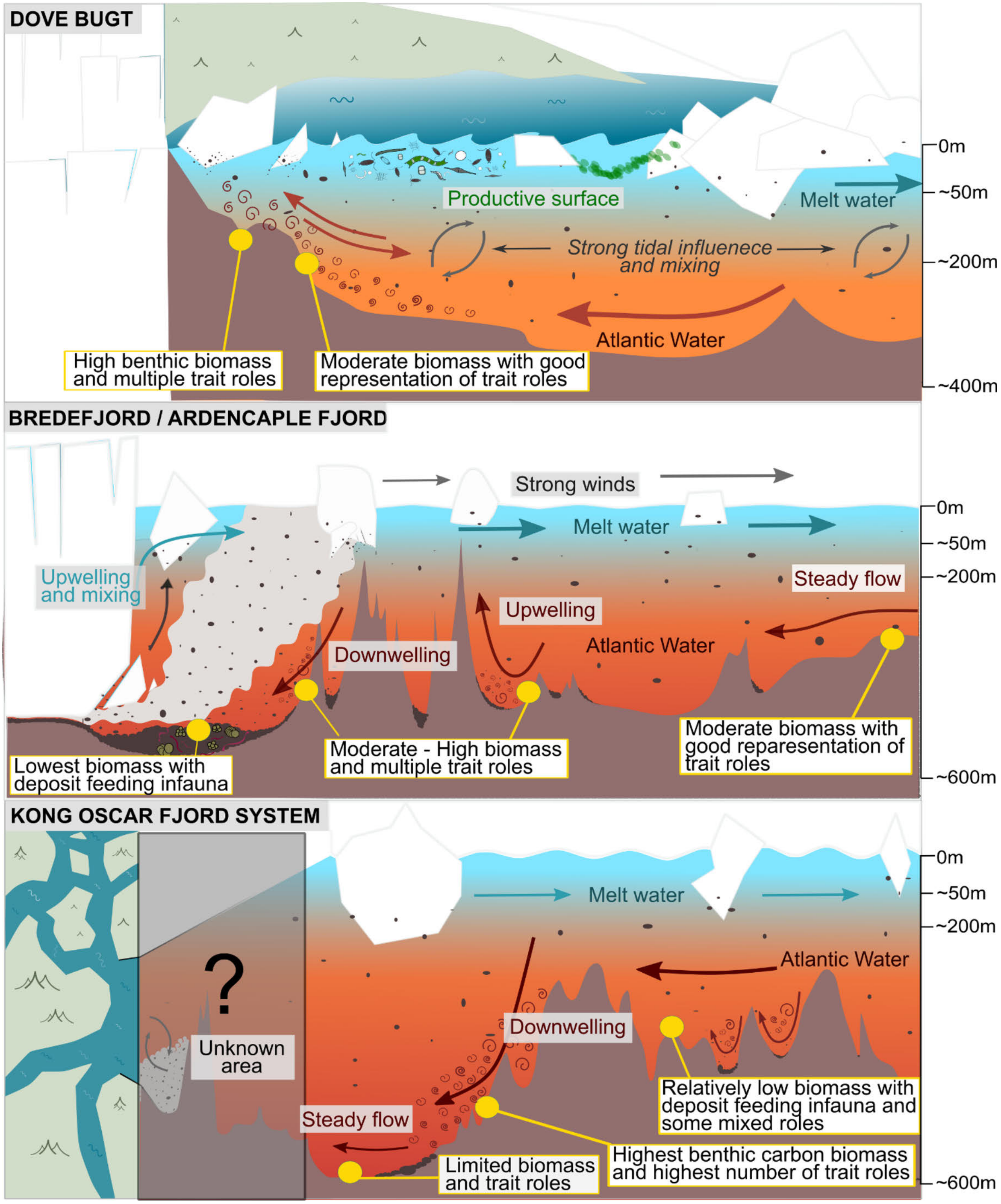
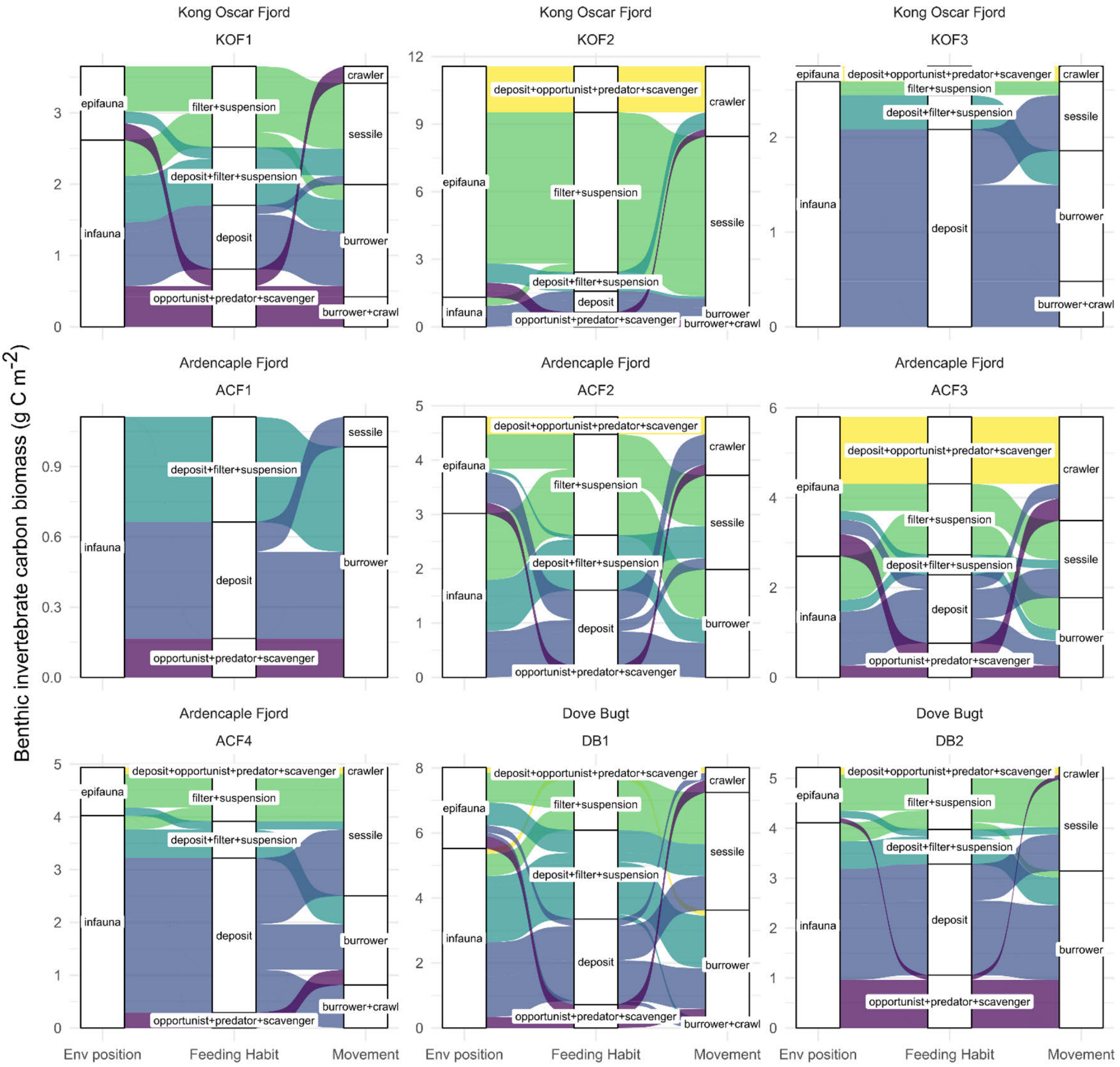


Figure S15. Enlarged benthic trait associations from Figs. 4-6 main text. Alluvial diagrams show the relationships among environmental position (infauna, epifauna), feeding habit (*e.g.*, deposit feeding, filter/suspension feeding, mixed strategies), and movement mode (*e.g.*, burrower, crawler, sessile). Each panel represents an individual station across Kong Oscar Fjord (KOF1–KOF3), Ardencaple Fjord (ACF1–ACF4), and Dove Bugt (DB1–DB2).



Phoebe Armitage

Arctic Benthic Seascapes

A trait-based perspective on benthic invertebrates around Greenland (Kalaallit Nunaat)

This thesis investigates macroinvertebrate communities living on the seafloor across an Arctic region undergoing rapid environmental change, where ecological knowledge remains limited. Going beyond species identity and the diverse communities these organisms form, it examines the behavioural, life history, and morphological traits that determine their ecological roles and interactions within the ecosystem. This work advances understanding of the processes structuring Arctic benthic ecosystems and their potential responses to climate change.

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