



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

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## Abstract

15 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  
20 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  
25 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  
30 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; Węśławski 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 Ardençaple 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

### 95 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.

100 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

110 Macrobenthic infaunal samples were collected aboard R/V *Maria S. Merian* in August 2022. Samples were collected using a box corer (1000 cm<sup>2</sup>), 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<sup>2</sup>. 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

120 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 (Węśławski 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,



125 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

### 130 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 135 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 140 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 145 sampled at 24 Hz. Data were processed following TEOS-10 standards to derive salinity, potential temperature ( $\theta$ ), 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,  $\theta = 0$ –7.5 °C), PW (salinity 26–34,  $\theta = -2$  to 2 °C), and AW (salinity 34–35.1,  $\theta = -1$  to 4 °C) (Gjelstrup et al. 2022).

150 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



155 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  
160 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  
165 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),  
170 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  
175 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  $\times$  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  
180 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 &  
185 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.

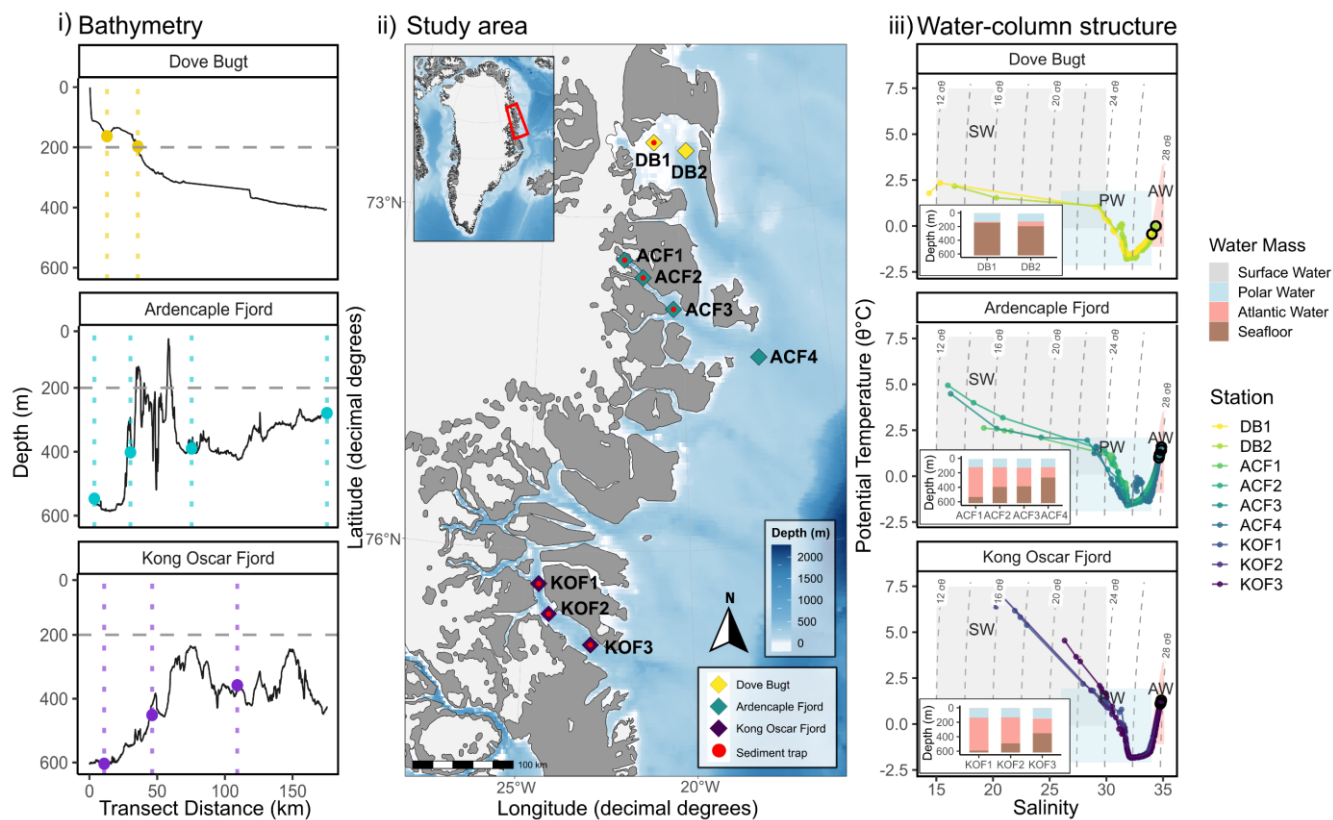
### 195 2.5.3 Post-hoc analyses of the latent variable gradient

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).

## 205 3. Results

### 3.1 Physical environment and water-mass structure

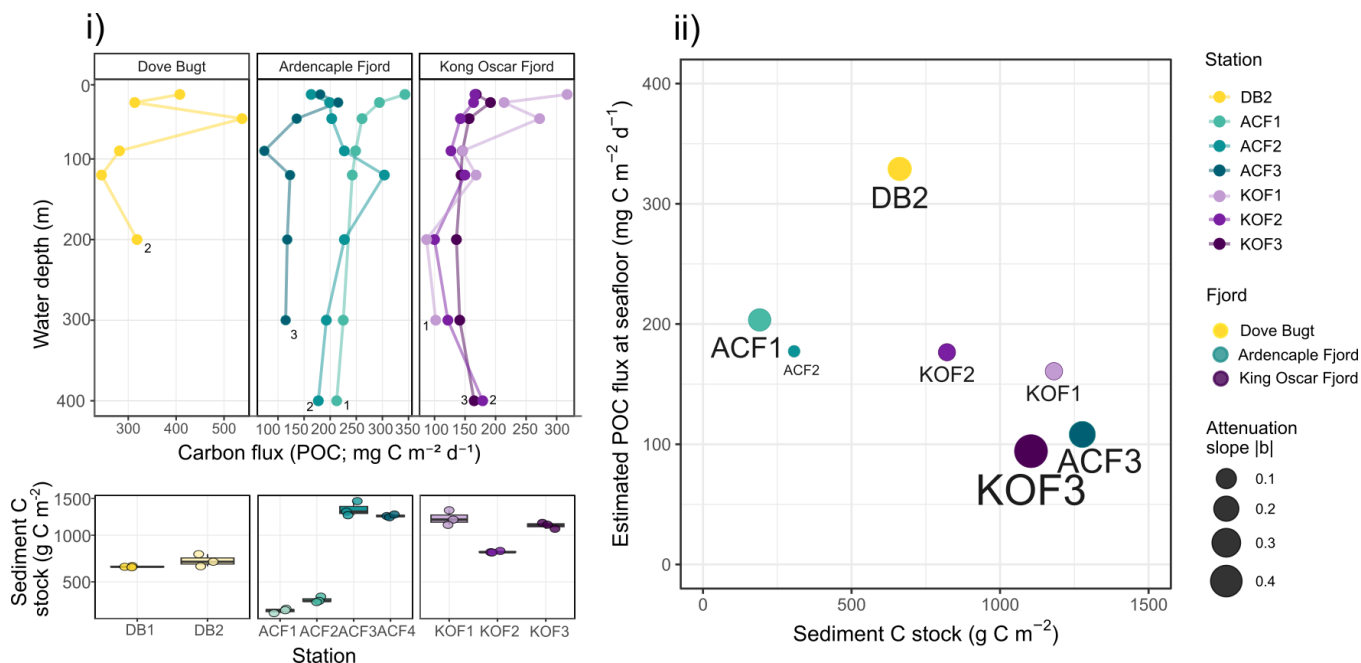
The water depth ranged from 50 m at the shallowest sill to approximately 600 m in Ardencaple and Kong Oscar Fjord; Dove Bugt is considerably shallower, reaching approximately 400 m with sampling stations at approximately 200 m. All three coastal systems showed a consistent three-layer water-mass structure 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 ( $\sigma_\theta$ ) 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,  $\text{mg C m}^{-2} \text{d}^{-1}$ ) 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 ( $\text{g C m}^{-2}$ ). (ii) Relationship between SOC ( $\text{g C m}^{-2}$ , x axis; log scale) and estimated POC flux at the seafloor ( $\text{mg C m}^{-2} \text{d}^{-1}$ , y axis; log scale). Symbols indicate the coastal system, coloured by transect position (inner, middle, outer). Symbol size denotes the attenuation slope  $|b|$ .

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Across the three coastal systems, the vertical POC export reaching the seafloor showed relatively moderate variation (threefold) among stations ( $\sim 110$  to  $\sim 320 \text{ mg C m}^{-2} \text{d}^{-1}$ ), 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 ( $318.3 \text{ mg C m}^{-2} \text{d}^{-1}$ ), compared to the Ardencaple Fjord and Kong Oscar systems, which averaged  $168.2 \pm 49.5$  and  $148.5 \pm 41.0 \text{ mg C m}^{-2} \text{d}^{-1}$  (mean  $\pm$  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 ( $212.4 \text{ mg C m}^{-2} \text{d}^{-1}$ ), through the mid-fjord station ( $177.3 \text{ mg C m}^{-2} \text{d}^{-1}$ ), to the outer station near the fjord mouth ( $114.7 \text{ mg C m}^{-2} \text{d}^{-1}$ ). In Kong Oscar Fjord, POC export followed a similar

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pattern to Ardencaple Fjord, with values around  $170 \text{ mg C m}^{-2} \text{ d}^{-1}$  at the inner and middle stations, declining to  $101.9 \text{ mg C m}^{-2} \text{ d}^{-1}$  at the outer, most open station.

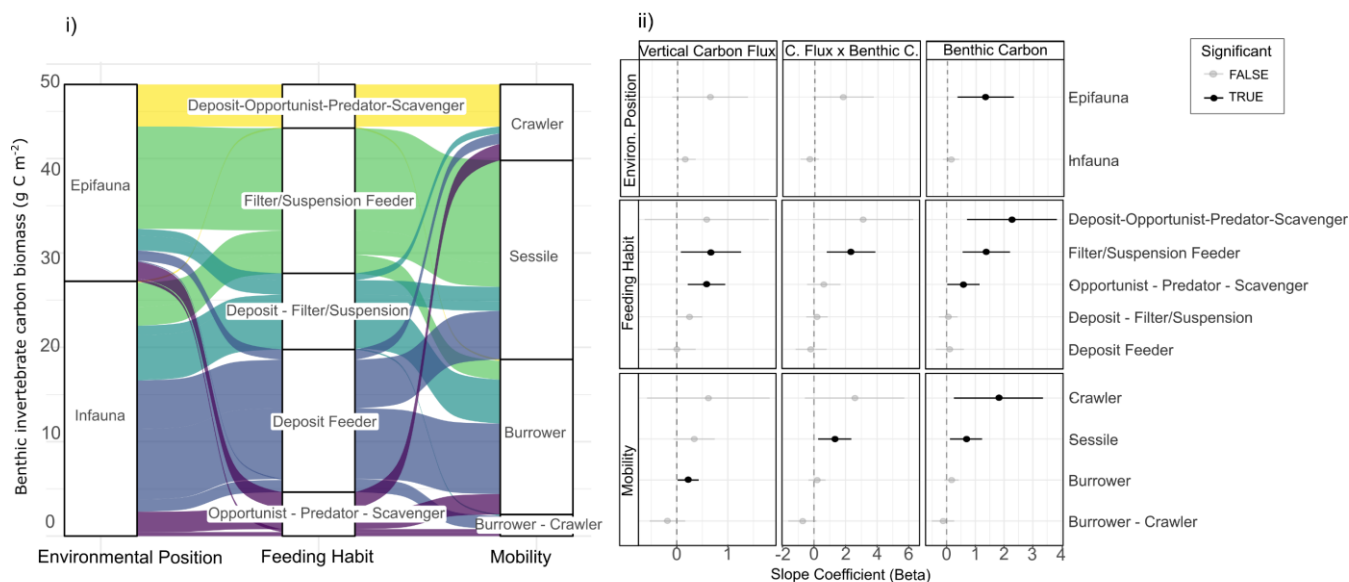
255 Surface SOC exhibited clear location-specific patterns rather than a consistent inner–outer gradient across systems (Fig. 2). In the Ardencaple Fjord system, SOC increased markedly from the inner fjord (ACF1,  $190.6 \text{ g C m}^{-2}$ ) through the mid-fjord station (ACF2,  $306.6 \text{ g C m}^{-2}$ ) to the outer fjord stations (ACF3,  $1,276.9$  and ACF4,  $1,206.5 \text{ g C m}^{-2}$ ), forming a pronounced spatial gradient. In contrast, Kong Oscar Fjord displayed a non-monotonic pattern, with relatively high SOC at KOF1 ( $1181.4 \text{ g C m}^{-2}$ ), lower values at KOF2 ( $821.3 \text{ g C m}^{-2}$ ), and elevated values again at KOF3 ( $1104.2 \text{ g C m}^{-2}$ ). SOC in Dove Bugt were comparatively uniform, with DB1 and DB2 exhibiting little spatial separation between stations ( $662.1$  and  $726.3 \text{ g C m}^{-2}$ ,  
260 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  
265 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 ( $1,181.4 \text{ g C m}^{-2}$ ) and ACF3 ( $1,276.9 \text{ g C m}^{-2}$ ), were associated with moderate vertical POC export at the deepest trap depth ( $164.9$  and  $114.7 \text{ mg C m}^{-2} \text{ d}^{-1}$ , respectively),  
270 whereas KOF3 exhibited one of the lowest POC export measurements ( $101.9 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) despite a relatively high SOC content in the sediment ( $1104.2 \text{ g C m}^{-2}$ ). Conversely, stations with higher POC export at depth, such as DB1 ( $318.3 \text{ mg C m}^{-2} \text{ d}^{-1}$ ), did not exhibit proportionally elevated SOC ( $726.3 \text{ g C m}^{-2}$ ).

### 3.3 Benthic biomass and dominant functional strategies

275 Across the region, nearly all benthic carbon biomass ( $\approx 95 \%$ ) 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).



280 **Figure 3 | Trait-based composition of benthic carbon biomass and trait-specific responses to carbon variables. (i)** The  
 distribution of benthic carbon biomass ( $\text{g C m}^{-2}$ ) 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) ( $\text{mg C m}^{-2} \text{d}^{-1}$ ) at the deepest sediment trap depth, the interaction  
 between vertical POC flux and SOC, and surface SOC. Points represent estimated coefficients ( $\beta$ ), with horizontal lines  
 285 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  
 290 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.

295 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



300 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.

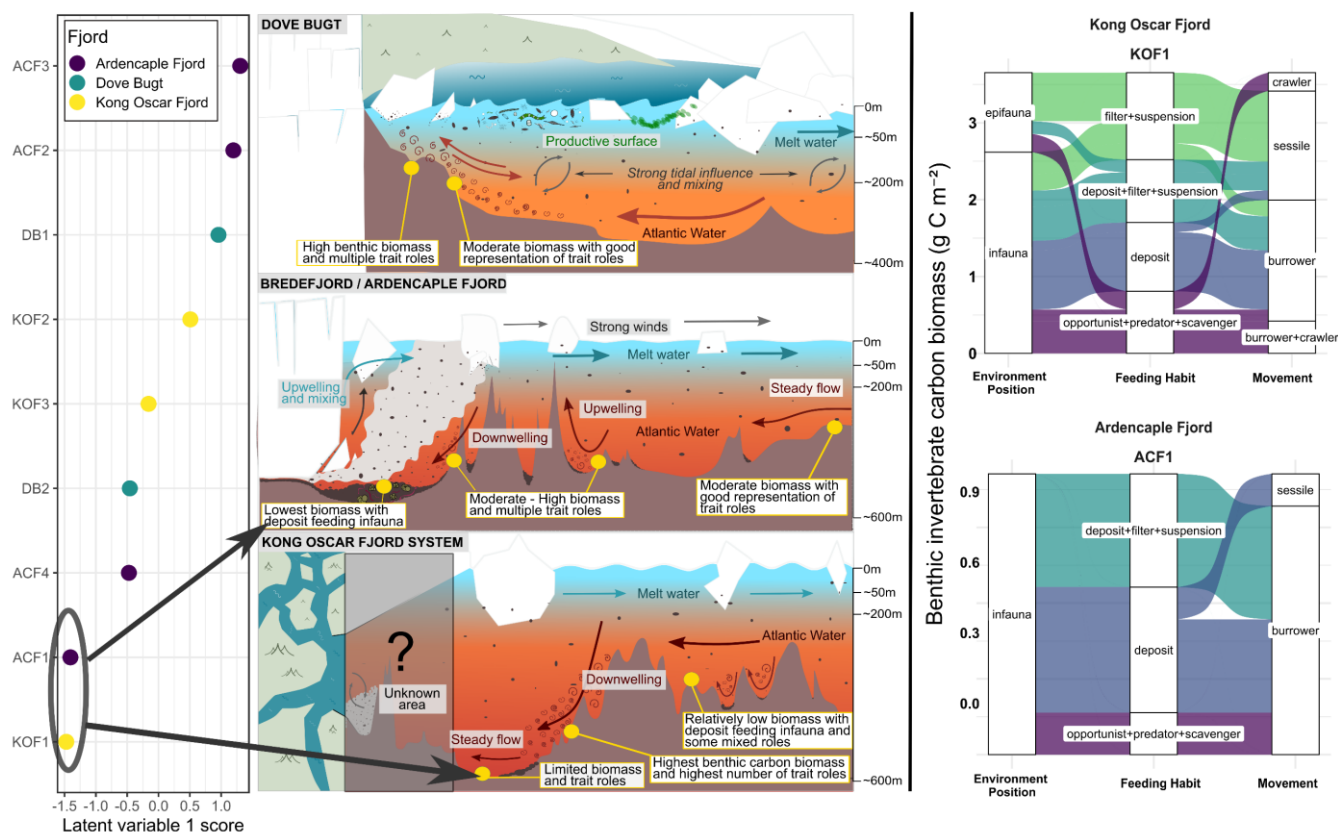
### 3.4 A latent hydrodynamic gradient shaping functional composition

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.

310 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 =  $3.65 \text{ g C m}^{-2}$  and ACF1 =  $1.11 \text{ g C m}^{-2}$ ; 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.



325

**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).

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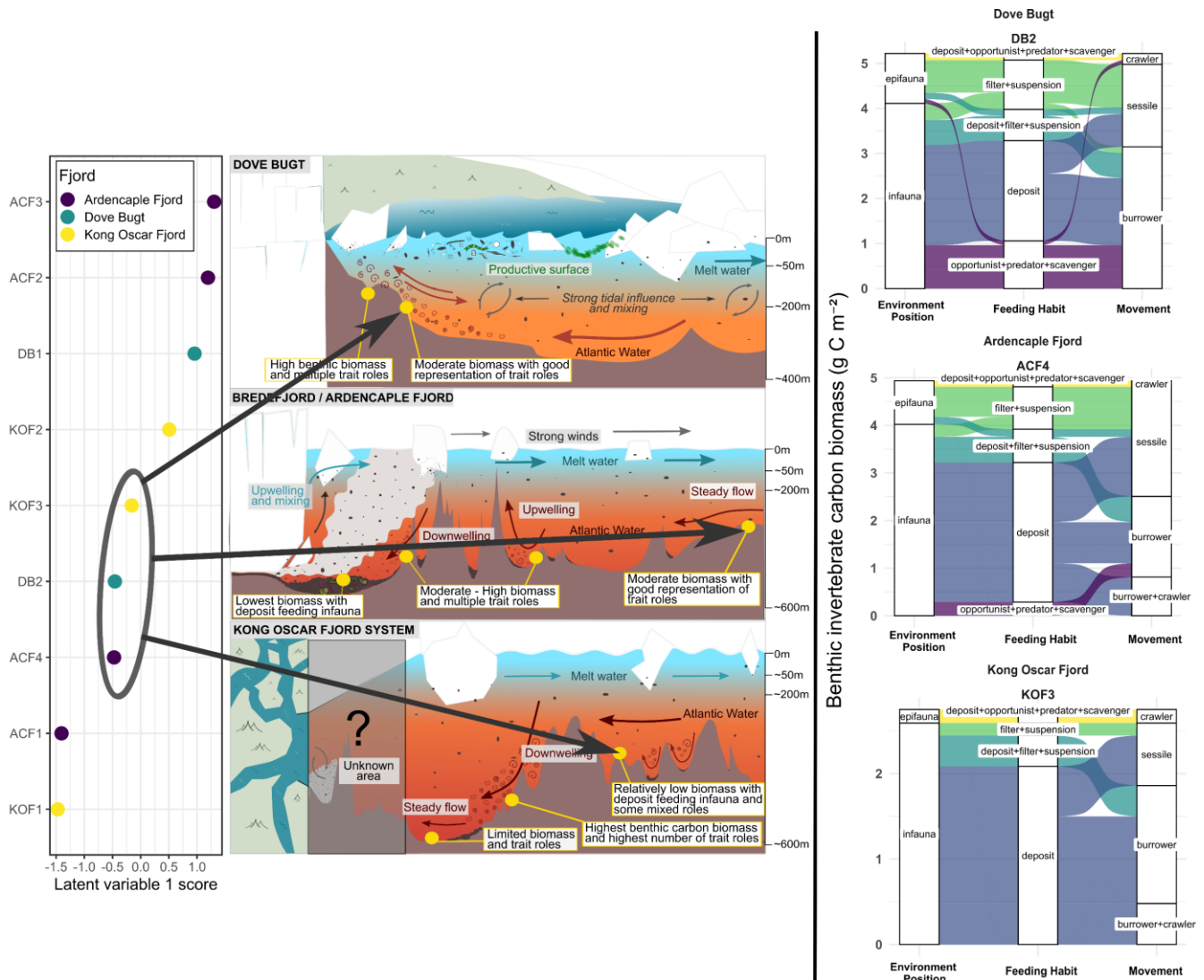
### 3.4.2 Intermediate LV1: stable seafloor habitats with moderate advection

Stations with intermediate LV scores (e.g., KOF3, DB2, ACF4) displayed intermediate benthic invertebrate biomass (KOF3 biomass = 2.75 g C m<sup>-2</sup>, DB2 = 5.22 g C m<sup>-2</sup> and ACF4 = 4.94 g C m<sup>-2</sup>) 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<sup>-2</sup>), yet DB2 displayed a broader representation of functional roles, indicating a more functionally heterogeneous

335



340 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.

345 **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.

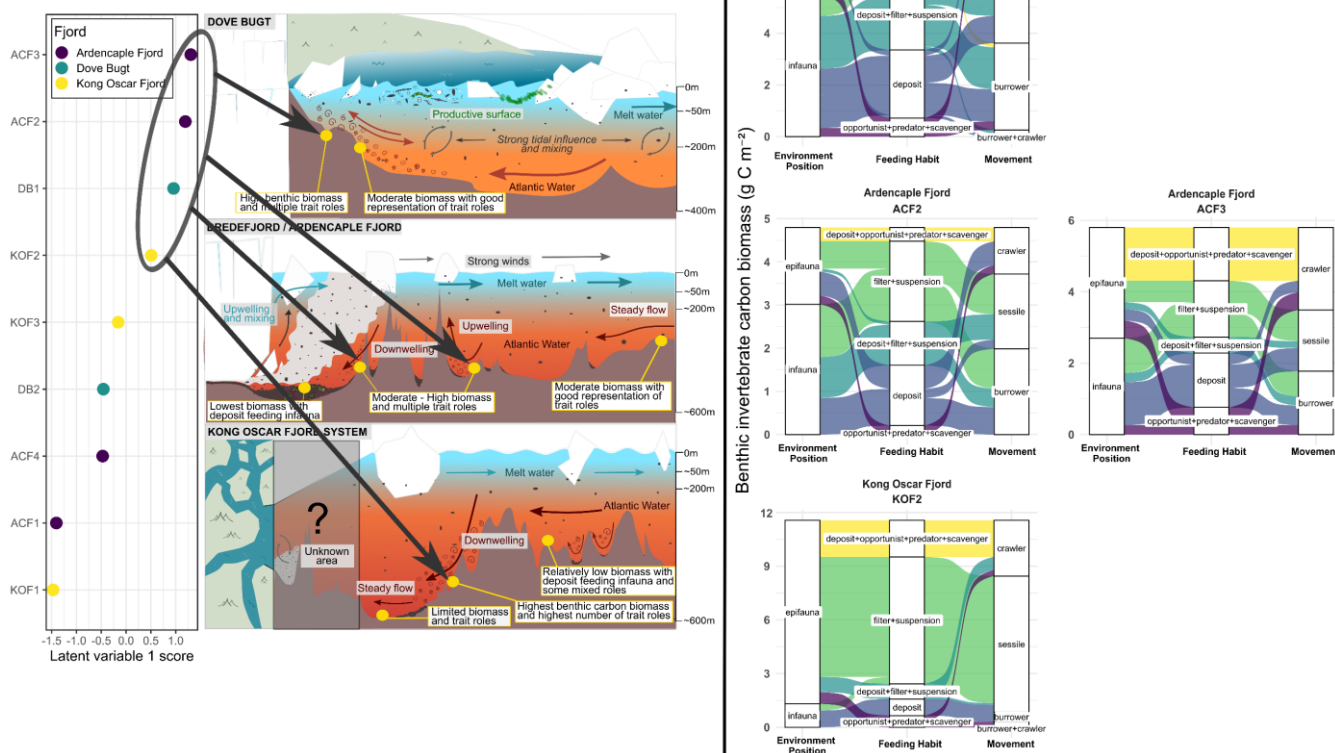


350 **High LV scores: advective, hydrodynamically exposed stations.**

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<sup>-2</sup>, ACF2 & 3 = 4.80 and 5.80 g C m<sup>-2</sup> and KOF2 = 11.6 g C m<sup>-2</sup>; 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

355 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

360 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



460 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, 465 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 470 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 475 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

480 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 485 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.

490 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 Ardençaple 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.

525 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  
530 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

535 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  
540 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  
545 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

550 The datasets supporting the findings of this study have been deposited in the FAIR aligned Zenodo repository and are available at <https://doi.org/10.5281/zenodo.20557795>. The repository contains all metadata necessary to reproduce the analyses presented in this study. Environmental and sediment trap data used in this study were originally published by Wiedmann and Svensen (2024) and are available through their associated repository (<https://doi.org/10.11582/2024.00040>). The version of



the sediment trap dataset included in the Zenodo archive has been reformatted solely to facilitate integration with the biological  
555 and environmental datasets used in the present study.

### 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  
560 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.

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