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Arctic benthos in the Anthropocene: Distribution and drivers of epifauna in West Greenland

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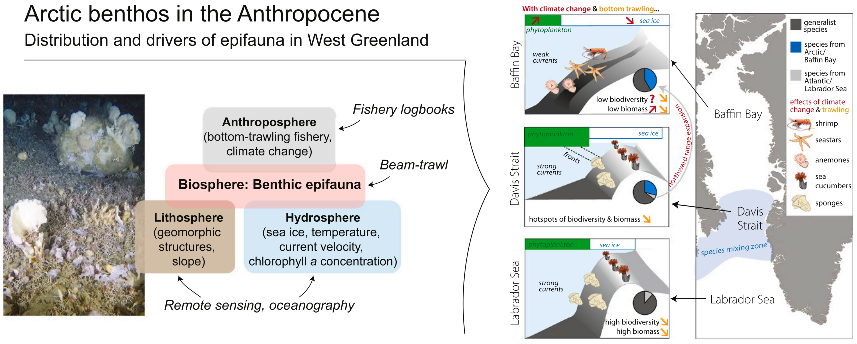
HIGHLIGHTS

- Epifauna data (biosphere) were combined with drivers from hydro- and anthroposphere.
- At high latitude, sea ice limits epifauna and filter feeders lack suitable habitats.
- Davis Strait forms a mixing zone for Arctic and Atlantic taxa and epifauna hotspot.
- Bottom-trawling has substantial adverse effects on epifauna biomass and biodiversity.
- Decreasing sea ice due to climate change may benefit epifauna in the north.

GRAPHICAL ABSTRACT



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ABSTRACT

Albeit remote, Arctic benthic ecosystems are impacted by fisheries and climate change. Yet, anthropogenic impacts are poorly understood, as benthic ecosystems and their drivers have not been mapped over large areas. We disentangle spatial patterns and drivers of benthic epifauna (animals living on the seabed surface) in West Greenland, by integrating an extensive beam-trawl dataset (326 stations, 59–75°N, 30–1400 m water depth) with environmental data. We find high variability at different spatial scales: (1) Epifauna biomass decreases with increasing latitude, sea-ice cover and water depth, related to food limitation. (2) In Greenland, the Labrador Sea in the south shows higher epifauna taxon richness compared to Baffin Bay in the north. The interjacent Davis Strait forms a permeable boundary for epifauna dispersal and a mixing zone for Arctic and Atlantic taxa, featuring regional biodiversity hotspots. (3) The Labrador Sea and Davis Strait provide suitable habitats for filter-feeding epifauna communities of high biomass e.g., sponges on the steep continental slope and sea cucumbers on shallow banks. In Baffin Bay, the deeper continental shelf, more gentle continental slope, lower current speed and lower phytoplankton biomass promote low-biomass epifauna communities, predominated by sea stars,

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anemones, or shrimp. (4) Bottom trawling reduces epifauna biomass and taxon richness throughout the study area, where sessile filter feeders are particularly vulnerable. Climate change with diminished sea ice cover in Baffin Bay may amplify food availability to epifauna, thereby increasing their biomass. While more species might expand northward due to the general permeability of Davis Strait, an extensive colonization of Baffin Bay by high-biomass filter-feeding epifauna remains unlikely, given the lack of suitable habitats. The pronounced vulnerability of diverse and biomass-rich epifauna communities to bottom trawling emphasizes the necessity for an informed and sustainable ecosystem-based management in the face of rapid climate change.

1. Introduction

Albeit remote, the seafloor of the Arctic seas is heavily impacted by fisheries and climate change (Clarke and Harris, 2003). Yet, due to the difficult and expensive accessibility, benthic community biomass, diversity and composition in the Arctic have only been patchily mapped (Bluhm et al., 2011; Jørgensen et al., 2022) and large knowledge gaps remain around Greenland. Therefore, distribution of benthic species in remote areas is often modeled, based on their respective environmental niches (e.g. Fabri-Ruiz et al., 2019). However, environmental controls are scale-dependent (Wiens, 1989), so patterns observed regionally are not necessarily transferable to large areas or vice versa (Guillaumot et al., 2020; Johannesen et al., 2017). In the Anthropocene, climate change shifts environmental controls at unprecedented rates, but effects on marine benthos are poorly understood (Wassmann et al., 2011). Whether we can predict benthic community distribution in large, remote areas of the Arctic based on available environmental information is therefore an important question from both an ecological and management point of view.

The West Greenland continental shelf and slope stretch from Cape Farewell (59°N) to northern Melville Bay (75°N), spanning a 2000 km latitudinal range over two seas, the Labrador Sea, an arm of the North Atlantic Ocean, and Baffin Bay, a marginal sea of the Arctic Ocean (Fig. 1A). The >325,000 km^2-large area is optimally suited to study spatial and environmental drivers and anthropogenic disturbance of polar benthos at different spatial scales, due to pronounced latitudinal gradients, separate biogeographic realms, complex marine landscapes, and ongoing bottom-trawling fisheries.

A strong, large-scale environmental gradient in the area is food supply to benthos that varies with water depth and latitude (Piepenburg, 2005). Most benthic ecosystems in shallow waters and the deep sea (>200 m water depth) rely on phyto- and zooplankton from the ocean surface for food (Danovaro et al., 2014; Maier et al., 2023; Smith et al., 2008). The availability of this particulate organic matter (POM) decreases with depth, curtailing the food supply to deeper benthic communities (Boyd and Trull, 2007; Lutz et al., 2002; Rex et al., 2006). Additionally, at higher latitude, sea-ice cover reduces light availability and shortens the phytoplankton growth season, limiting benthic food supply (Mundy et al., 2014; Oziel et al., 2019). In West Greenland shelf waters, net primary production decreases by a factor of two to three from south to north (Vernet et al., 2021). However, sea-ice algae aggregates can provide an important food pulse for Arctic benthos (Boetius et al., 2013; Roy et al., 2014; Søreide et al., 2010; Yunda-Guarin et al., 2020). Furthermore, the interaction of (tidal) currents and steep topography, such as oceanic banks, sills (including Davis Strait), or the continental slope, can enhance vertical mixing, thereby boosting local primary productivity (Schulz et al., 2022) and accelerating downward food transport (Mohn et al., 2014; van der Kaaden et al., 2023).

Biogeographic patterns of benthic invertebrates arise when their larval dispersal is restricted e.g., by ocean currents, regionally-confined water masses, or bathymetric features (Gaylord and Gaines, 2000; Schulz et al., 2020; Wiens, 2011) or when environmental niches change over space (Wiens, 2011). In West Greenland, Davis Strait between the Labrador Sea in the south and Baffin Bay in the north (Fig. 1A) is considered as important biogeographic border, separating North Atlantic from boreal and Arctic fauna (Costello et al., 2017; Victorero et al., 2023). Only at depth (200–400 m), warm, saline Atlantic water (subpolar mode water, i.e. SPMW) passes Davis Strait and flows northwards to Melville Bay, while in the upper water column, the Atlantic water mass is deflected westward (Fig. 1C; Rysgaard et al., 2020; Mortensen et al., 2022). The presence of several water masses in Davis Strait, i.e. Southwest Greenland Coastal Water, Baffin Bay Polar Water, and SPMW, generates pronounced hydrographic fronts which have been associated with high pelagic productivity (Laidre et al., 2010; Munk et al., 2003).

Geomorphic structures define marine landscapes and benthic habitats on a regional scale (Harris and Baker, 2012). In West Greenland, deep troughs (>500 m water depth) incise the continental shelf and alternate with shallow banks (<100 m), deeper plains or rugged terrain (100–500 m) with small-scale features such as bedrock ridges and cross-cutting channels (Batchelor et al., 2018; Hofmann et al., 2016; Krawczyk et al., 2022). In the Labrador Sea and Davis Strait, the Greenland continental shelf is relatively shallow and narrow (on average 170 m deep, 40–130 km wide), characterized by a steep continental slope (Fig. 1A). In Baffin Bay, the Greenland continental shelf is deeper and wider (ca. 380 m deep, 120–250 km wide), with deep troughs and a gentler continental slope (Fig. 1A). Troughs, plains and deep-sea basins in the area are often filled with mixed, soft or muddy sediments, while (mixed) hard substrate such as bedrock often occurs on banks, rugged terrain or slopes (Gougeon et al., 2017; Krawczyk et al., 2022). Sandy and rocky habitats with high current speed are more prominent in Southwest Greenland, while in the north, muddy habitats prevail (Gougeon et al., 2017). Soft, muddy substrate provides a habitat for benthic burrowers or crawlers that move in the sediment and at the sediment surface and feed on detrital material (deposit-feeders; Degen and Faulwetter, 2019). Sessile, filter-feeding epifauna i.e., animals living on the seabed surface such as sponges, anemones, soft corals, hydrozoans and bryozoans, often prefer hard substrate (Yesson et al., 2015).

Anthropogenic and natural disturbances of Arctic marine ecosystems act on small to large spatial and temporal scales. The Arctic is warming much faster than the rest of the globe (Holland and Bitz, 2003; Rantanen et al., 2022), leading to unprecedented rates of sea ice loss, melting of glaciers and the Greenland Ice Sheet (Abdalati and Steffen, 2001; King et al., 2020). Bottom-trawling fisheries, in West Greenland mostly for northern shrimp (*Pandalus borealis*) and Greenland halibut (*Reinhardtius hippoglossoides*), degrade the benthic habitat and remove particularly the large, sessile epifauna (Blicher and Hammeken, 2021; Jørgensen et al., 2016; Yesson et al., 2017). In addition, natural disturbance of benthos is caused by iceberg scouring, that can reach down to 600 m depth (Gutt, 2001; Krawczyk et al., 2022; Yesson et al., 2017). Large- and small-scale alterations of environmental conditions affect the Arctic marine ecosystem, with yet largely unknown consequences for Arctic benthos and local communities relying on them (Wassmann et al., 2011).

Here, we use an epifauna dataset from 326 stations in West Greenland, covering a large latitudinal range (59–75°N) and depth gradient (30–1400 m), to examine the following hypotheses:

(1) Epifauna communities vary at different spatial scales, shaped by a combination of environmental drivers and anthropogenic disturbance.

(2) Epifauna biomass decreases with increasing latitude (2000 km) and depth (30–1400 m) due to food limitation.

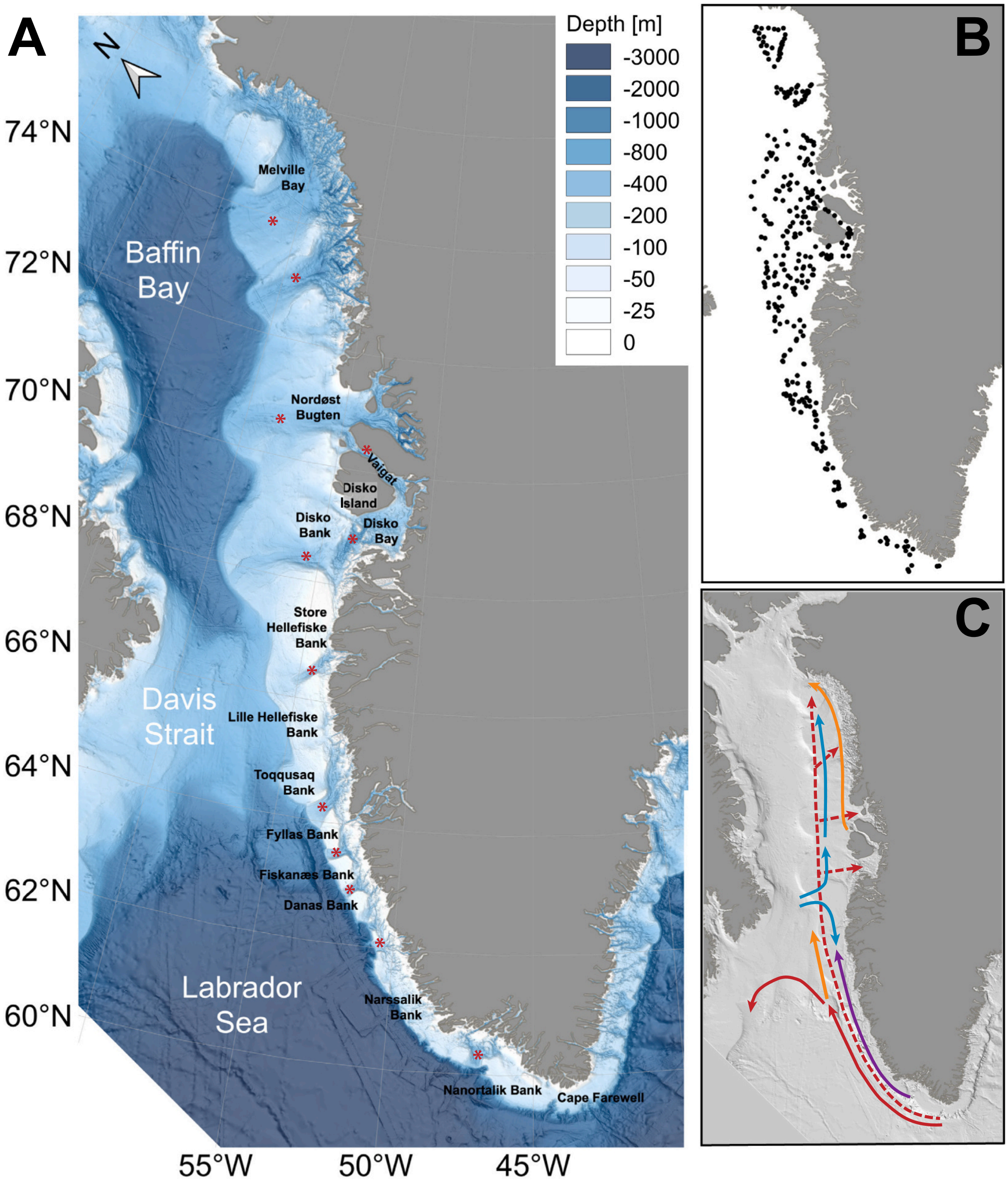

Fig. 1. A: Study area, the West Greenland continental shelf and slope, stretching from Cape Farewell in the south to Melville Bay in the north, encompassing the Labrador Sea, the interjacent shallower Davis Strait and Baffin Bay. Banks are indicated by name, troughs by red asterisks (bathymetry map from IBCAO version 4, resolution: 200 × 200 m, Jakobsson et al. 2020a; b). B: Beam trawl stations. C: Currents, modified from Rysgaard et al. (2020). Solid lines: surface water; dashed lines: deep water; red: Subpolar Mode Water (SPMW) of Atlantic origin; orange: diluted water; blue: Baffin Bay Polar Water (BBPW); violet: Southwest Greenland Coastal Water (CW).

(3) Epifauna communities differ between the Labrador Sea and Baffin Bay (scale of 500–1000 km) with Davis Strait as biogeographic boundary.
(4) Epifauna communities differ between regions (100–500 km) and geomorphic structures (10–100 km) due to specific marine landscapes.

Based on this evaluation, we discuss how predictable and vulnerable benthic communities are in vast, understudied areas such as Greenland.

2. Materials and methods

2.1. Epifauna data

Benthic fauna were sampled with a beam trawl (2.5 m opening, 10 mm mesh size in the cod-end) at 326 stations (Fig. 1B) between 2015 and 2019, during cruises of the RV Paamiut, RV Sanna and FT Helge Maria. The beam trawl was towed over ground for 0.34 ± 0.16 km (mean ± standard deviation), 6 ± 2 min at a speed of 1.7 ± 0.8 kn, covering a swept area of 860 ± 417 m^2. Fauna samples were sorted and identified directly aboard to the lowest-possible taxonomic level (Table B.1, taxonomy based on the World Register of Marine Species WoRMS, Ahyong et al., 2023). Taxonomically-sorted fauna samples were let drip from excess water, counted and weighed on a fine balance (wet mass). It should be noted that sampling by beam trawling catches mostly epifauna (and not infauna, Reiss et al., 2006), hence we refer to epifauna throughout.

A subset of epifauna samples (1–9 per genus, as available) was kept at −20 °C to derive taxon-specific conversion factors from wet mass to ash-free dry mass (AFDM). Samples were dried at 60 °C until constant weight (2–42 days) and weighed again at room temperature (dry mass). Dry samples were combusted at 480 °C for 24–48 h. The remaining ash was weighed at room temperature. AFDM was calculated as dry mass minus ash mass. If no conversion factor from wet mass to AFDM was available for one taxon (not all taxa were sampled), the average conversion factor from the next-lower taxonomic level was used.

Pelagic taxa were removed from the dataset (Table B.2). To avoid analytical bias due to identification to different taxonomic levels, records were truncated to genus level or, if unavailable, to the lowest common taxonomic level (Hawes et al., 2020, Table B.1, ‘assigned taxon’). For groups with a relatively mixed taxonomic resolution, we maintained the lower taxonomic level where trusted. For example, records of frequent sponge genera were maintained and records identified only to phylum level were reported as ‘Porifera-unidentified’.

2.2. *Spatial patterns*

Spatial patterns were considered at different scales: (1) latitude across the entire study area (59–75°N, 2000 km), (2) seas (Labrador Sea <62°N, Davis Strait 62–67°N, Baffin Bay >67°N; Fig. 1A), (3) regions (100–500 km, Fig. 2A), (4) smaller scales, i.e. within-regions (10–100 km), (5) water depth (30–1400 m). Spatial scale is represented numerically by latitude, depth, and by Moran Eigenvector Maps (MEMs; Dray et al., 2012). MEMs describe the position of each station in relation to all other stations as distance-based eigenvector maps, from the broadest scale (MEM 1: maximum extension of the study area: 2000 km) to the finest scale (MEM 37: minimum distance between neighbouring stations: 0.26 km). MEM1 was excluded as it corresponds to latitude. MEM2 to MEM3 roughly represent the scale of different seas, MEM4 to MEM6 the regional scale, and MEM7 to MEM37 the scale within regions. MEMs can be used as spatial predictors in statistical models to account for spatial autocorrelation and to detect patterns on respective spatial scales. MEMs were generated in R from a distance-based connectivity matrix (package *adespatial*, Dray et al., 2022; van der Kaaden et al., 2023).

2.3. *Environmental drivers and anthropogenic disturbance*

Environmental drivers include geomorphic structures, slope of the terrain, temperature, current velocity, chlorophyll *a* concentration of surface water, and number of sea-ice covered days. For temporally-variable data, we chose means of 2014–2018 (where available, Table 1), i.e. one year prior to the first and last benthos sampling, assuming that these reflect the most recent/current effect on benthic communities. Longer-term effects could not be considered due to a lack of long-term environmental data.

We identified six qualitative geomorphic structures based on seabed topography, depth, hillshade, and slope analyses from the IBCAO bathymetry grid (IBCAO version 4, obtained by interpolation of measured data at a resolution of 200 × 200 m; Jakobsson et al., 2020a, 2020b).

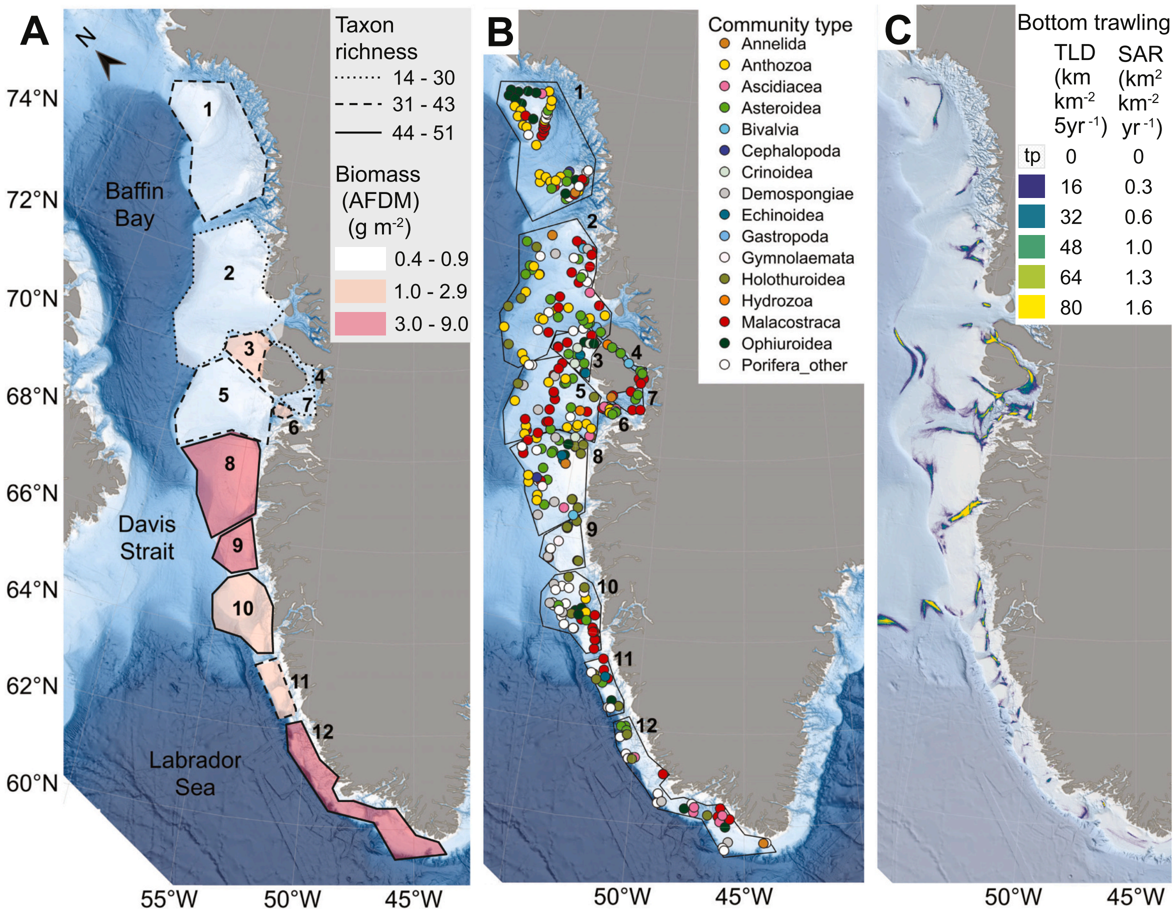

Fig. 2. Distribution of epifauna biomass, taxon richness and community types in the regions of the West Greenland shelf and slope and relation with bottom-trawling footprint. A: Biomass (station mean of AFDM, indicated by area fill) and taxon richness (station mean, indicated by area stroke). Data available in Table B.6. B: Community type (taxonomic group predominant in AFDM). C: Bottom trawl line density from 2014 to 2018; zoomed-in maps are provided as Fig. A.4. Regions: (1) Melville Bay, (2) Upernavik & Nordøstbugten, (3) West of Disko Island, (4) Vaigat, (5) Disko Bank, (6) outer Disko Bay, (7) inner Disko Bay, (8) Store Hellefiske Bank, (9) Lille Hellefiske Bank, (10) Toqqusaq & Fyllas Bank, (11) Fiskenæs & Danas Bank, (12) Southwest Greenland.

Table 1
Overview on the investigated epifauna parameters in relation to environmental drivers and anthropogenic disturbance through bottom-trawling. Indicated are data origin, year, and data transformation for statistical analyses.

Parameter	Abbreviation	Data origin	Years	Data transformation
Epifauna biomass (Ash-free dry mass, in $g\,m^{-2}$)	afdm	Beamtrawl dataset, GINR	2015–2019	log
Epifauna taxon richness	richness	Beamtrawl dataset, GINR	2015–2019	none
Latitude	lat	Beamtrawl dataset, GINR	NA	none
Moran Eigenvector Maps	MEMs (2–37)	Largest to smallest spatial scale of beamtrawl dataset	NA	none
Water depth (m)	depth	Ship record	NA	log
Slope (°)	slope	IBCAO version 4 [1]	NA	log
Geomorphic structure	morph	Categories derived from IBCAO v4 (depth, terrain features)	NA	as factor
Temperature (°C)	T	Mean of measured bottom temperature (beam trawl dataset) & nearby CTD profiles	2014–2018/2019	none
Current velocity ($m\,s^{-1}$)	v	Model: The Arctic Subpolar Gyre sTate Estimate (ASTE Release 1) (annual mean of daily model output) [2]	mean 2014–2017	log(v+0.01)
Chlorophyll *a* concentration surface water ($mg\,m^{-3}$)	chl	Satellite, OCCI Oceancolour remote sensing [3]	mean 2014–2018	none
Number of sea-ice covered days per year (days)	sea ice	Satellite, IFREMER	mean 2014–2018	none
Bottom trawl-line density ($km\,km^{-2}\,5\,yr^{-1}$)	tld	Haul-by-haul logbook data, Greenland Fishery Licence Control (GFLK)	sum 2014–2018	boxcox ($\lambda = -2$)
Swept area (confounding factor, km^2)	area	Beamtrawl dataset, GINR	NA	log
Sampling year (confounding factor)	year	Beamtrawl dataset, GINR	2015–2019	none

[1] Jakobsson et al., 2020a, 2020b.
[2] Nguyen et al., 2021
[3] Sathyendranath et al., 2019.

Slope (in °) and hillshade were computed in QGIS (version 3.22.9-Białowieża), using the slope (z-factor = 1) and hillshade algorithms. The resulting broad terrain structures align with the Greenland Ocean floor Classification of Habitats (Krawczyk et al., 2021b) and the broad-scale geomorphology in the area (Dowdeswell et al., 2016; Ryan, 2013): bank (<100 m water depth, on a crest, plateau or rugged terrain on the continental shelf), plain (>100 m–500 m water depth, flat terrain on the continental shelf), rugged terrain (>100 m–500 m water depth, rugged terrain and slopes on the continental shelf), trough (>500 m water depth, flat terrain or depression in a trough on the shelf), continental slope (varying water depth, 0.5–17° slope), deep-sea off-shelf (flat, deep-sea terrain behind the continental slope, only sampled in Davis Strait). Bottom-temperature, a proxy of water mass was measured during most beam-trawl deployments (295/326 stations) with a Starmon temperature logger. Additional bottom-temperature data were available from CTD casts near 247 beam trawl stations (0.5–65 km distance, maximum 100 m depth difference, 1–9 casts between 2014 and 2018; ICES Dataset on Ocean Hydrography). To obtain values for all stations, we used the mean temperature from beam-trawl deployments and CTD casts. Bottom-water current velocity estimates (in $m\ s^{-1}$) were obtained from the Arctic Subpolar Gyre sTate Estimate model (ASTE Release 1) at the grid point closest to each beam-trawl station at daily resolution (Nguyen et al., 2021; resolution ca. 15 km, Disko Bay not resolved). As the model does not account for tides, current velocity variability is underestimated. The number of sea-ice covered days per year (>70 % of ocean surface covered by sea ice) was derived from satellite images, provided by IFREMER (resolution 12.5 km). Monthly-averaged surface chlorophyll *a* concentration [in $mg\ m^{-3}$], a proxy of surface phytoplankton biomass, was obtained from satellite data (OCCI Oceancolour remote sensing) (Sathyendranath et al., 2019), averaged over each year and finally over 2014–2018.

To assess anthropogenic disturbance from bottom-trawling fishery, commercial bottom trawl lines from 2014 to 2018 were mapped separately for every year (2014–2018) in QGIS (projection UTM zone 32622), based on haul start and end coordinates in logbook data from the Greenland Fishery License Control (GFLK). Trawl line density ($km\ km^{-2}\ 5\ yr^{-1}$) was calculated from the trawl lines 2014–2018 summed within a circular neighborhood of 1 km radius, corresponding to an area of 3.14 km^2, using the QGIS Line density tool. For comparability with other studies, trawling intensity is additionally indicated as SAR (swept area divided by surface area grid cell, in $km^2\ km^{-2}\ yr^{-1}$). For SAR estimation, trawl line density was multiplied by 100 m (0.1 km), the average gear width in similar European fisheries (Amoroso et al., 2018), and divided by 5 years (2015–2018). As rough estimate, SAR is only indicated alongside trawl line density. Note that other types of fisheries are present in the area, in particular Greenland halibut fishery using gillnets and longlines in Disko Bay (Nygaard, 2023) and occasionally further offshore (Nogueira and Hedges, 2023), which may affect benthic fauna locally (Buhl-Mortensen et al., 2005). However, in this study we focus exclusively on bottom trawling as the overall dominant fishing activity in the area.

2.4. Analysis of epifauna biomass and taxon richness

Total epifauna biomass (AFDM) and taxon richness, a measure of biodiversity, were calculated for every station. Total biomass was standardized to swept area (in m^2). For taxon richness, singletons (taxa only recorded at one station) were removed due to their sensitivity to random fluctuations (Roy et al., 2014). As taxon richness did not increase with swept area, indicating saturated species accumulation curves, taxon richness was not standardized to swept area. It should be noted that we specifically target epifauna here, neglecting infauna which contribute to total benthic diversity and biomass.

Epifauna biomass and taxon richness were mapped at scales of latitude, depth, and regions. To identify regions of high versus low epifauna biomass and/or taxon richness, regions were grouped as follows: low biomass: 0.4–0.9 g AFDM m^{-2}, medium biomass: 1–2.9 g AFDM m^{-2}, high biomass: 3–9 g AFDM m^{-2}; low taxon richness: 14–30, medium taxon richness: 31–43, high taxon richness: 44–51. Multifactorial linear regression (R Core Team, 2020) was used according to Kassambara

(2018) and Zuur et al. (2010) to assess the relation between total epifauna biomass and taxon richness (response variables) with their potential drivers (predictor variables) latitude, water depth, slope, geomorphic structure, temperature, current velocity, chlorophyll *a* concentration, sea-ice covered days, bottom trawl line density, MEMs 2–37 (spatial predictors), swept area and sampling year (confounding effects; Table 1). All response and predictor variables were checked for normal distribution by histograms, data fitting to a theoretical normal distribution via maximum likelihood estimation (package *fitdistrplus*, Delignette-Muller and Dutang, 2015), and goodness of fit assessment (empirical versus theoretical distribution and cumulative distribution function, Q-Q plot, P—P plot). Not normally-distributed variables were log- or boxcox-transformed to approach normal distribution (Table 1, Fig. A.1). For each response variable, a full linear model with all potential drivers was fitted first. Predictors were removed by stepwise backward model selection until the lowest model AIC (Akaike Information Criterion) was reached. To avoid collinear predictors in the final model, generalized variance inflation factors (GVIF) were calculated (Fox and Weisberg, 2019). Predictors with $\mathrm{GVIF}^{1/(2\cdot\mathrm{degrees\ of\ freedom})} > 3.16$ were stepwise removed. Residuals of the final model were checked (residuals versus fitted values, Q-Q plot). The relative importance of drivers in the final model was assessed with a variance decomposition metric (LMG) (Groemping, 2007), calculating the relative contribution of each predictor to the overall R square.

2.5. *Analysis of epifauna community composition*

Analyses of epifauna community composition were carried out at different levels of complexity (community types, traits, assigned taxa, individual species) as follows.

2.5.1. *Spatial patterns of epifauna community composition*

To assess the general degree of spatial variability, community similarity (1–Bray-Curtis dissimilarity; Oksanen et al., 2020) was plotted over distance between sampling stations. Epifauna communities at all stations were then classified into 'community types', defined by the taxonomic group (Table B.4) predominating in biomass (AFDM) ('predominant taxonomic groups'). This classification was chosen because at most stations, one taxonomic group predominated (Fig. A.2). Community types were mapped and their environmental niches were described as the conditions at sites of occurrence.

2.5.2. *Drivers of epifauna community composition*

Environmental drivers and spatial patterns of community composition were identified in a constrained (i.e. canonical) correspondence analysis (CCA), using log-transformed AFDM of 'assigned taxa' (Table B.1) and following the procedure by Oksanen et al. (2020) and Zelený (2023). The global CCA model included all environmental and spatial predictors (see Table 1). Collinear predictors with variance inflation factors (VIF) >10 were excluded. The best-fitting model was determined by stepwise forward model selection for lowest AIC. CCA significance (ordination, axes, predictors) was tested with permutation tests, with *p*-values corrected for false discovery rate indicating significance of predictors at $p < 0.05$. Constrained co-inertia in relation to total inertia was interpreted as measure of explained variance in community composition. CCA results were visualized as stations colored by community type.

2.5.3. *Epifauna feeding and movement traits*

Epifauna taxa were grouped into feeding traits (deposit feeder, filter feeder, predator) and movement traits (burrower, crawler, sessile, facultatively swimming) (Table B.1), based on the Arctic Traits Database (Degen and Faulwetter, 2019) plus information collected by an expert working group within the Long-Term Benthos Monitoring network (Jørgensen et al., 2017); for some non-registered taxa, information was available from the World Register of Marine Species (Ahyong and et al., 2023). Taxa with mixed or non-available classification were pooled as 'rest'. The biomass of trait groups was compared between shallow (<200 m) and deep (>200 m), between the Labrador Sea, Davis Strait, and Baffin Bay, and between categories of bottom-trawling impact (no trawling, low impact: >0 - <0.6 km km^{-2} $5\mathrm{yr}^{-1}$, high impact: 0.6–28.7 km km^{-2} $5\mathrm{yr}^{-1}$). Significant differences ($p < 0.05$) were identified by Kruskal-Wallis rank sum tests (R Core Team, 2020) and posthoc Dunn's Tests of Multiple Comparisons (Signorell et al., 2021).

2.5.4. *Davis Strait as biogeographic boundary*

To evaluate whether Davis Strait is a biogeographic boundary for epifauna distribution, we assessed each species' latitudinal distribution range (southern-most to northern-most record) and occurrence in different seas (Labrador Sea, Baffin Bay, Davis Strait). In addition, differences in community composition between the Labrador Sea and Baffin Bay were analyzed by non-metric multidimensional scaling (NMDS biplots) and Analysis of Similarities (ANOSIM) (Oksanen et al., 2020), using log-transformed AFDM of 'assigned taxa' (Table B.1).

3. Results

3.1. *Epifauna biomass and taxon richness*

A total of 464 epifauna taxa within 277 families were recorded on the West Greenland continental shelf and slope (Table B.1). Epifauna communities show a strong variability on all spatial scales, as hypothesized. Epifauna biomass ranges between 0.01 and 242 g AFDM m^{-2} (0.08–1549 g WM m^{-2}). Epifauna taxon richness ranges from 4 to 87 taxa per station. Epifauna biomass and taxon richness generally decrease with increasing latitude (scale 2000 km) and sea-ice cover, except for a local maximum of taxon richness and biomass around Davis Strait between 62 and 67°N (Fig. 3, Table 2). Epifauna biomass in Melville Bay (northern Baffin Bay) is seven times lower than in the Labrador Sea. At the same time, annual sea ice in Melville Bay persists for 1–2 months and the surface chlorophyll *a* concentration is ca 2–3 times lower compared to those regions in the Labrador Sea that remain ice-free throughout the year (Fig. A.3). Epifauna biomass decreases with water depth, while taxon richness increases from 30 m to 150 m and decreases below.

Some regions (scale 100–500 km) form epifauna 'hotspots' of high biomass and taxon richness e.g., the Store Hellefiske Bank at the transition of Davis Strait to Baffin Bay (67–68°N), and Southwest Greenland (Fig. 2A, B). High biomass is mostly driven by sea cucumber-dominated communities (Holothuroidea) on the Store Hellefiske Bank, and by sponge-dominated communities (Demospongiae, Porifera_other) in Southwest Greenland (Fig. 2B). In contrast, epifauna 'coldspots' of low biomass and taxon richness occur in the inner Disko Bay, Vaigat, Upernavik and Nordøstbugten. Presence of these regional patterns is confirmed by significant correlation of biomass ($p = 0.0003$) and taxon richness ($p = 0.02$) with MEM4, reflecting a distance of ca. 500 km.

Within regions (scale 10–100 km), epifauna biomass and taxon richness vary significantly between geomorphic structures (Fig. 3D, 2I; $p < 0.05$; exact *p*-values in Table B.5). This regional spatial pattern is confirmed by significant correlation of biomass and taxon richness with MEMs that roughly reflect distances between geomorphic structures, i.e. MEM6 (100–150 km), MEM12, and MEM15 (50–100 km). Epifauna biomass is highest on banks (10.7 ± 37.1 g AFDM m^{-2}; mean ± SD) and comparatively low on plains (0.5 ± 0.5 g AFDM m^{-2}), in the deep-sea off the shelf in Davis Strait (0.9 ± 0.7 g AFDM m^{-2}), in troughs (1.1 ± 1.6 g AFDM m^{-2}), on rugged terrain (0.8 ± 1.2 g AFDM m^{-2}), and on the continental slope (1.8 ± 3.3 g AFDM m^{-2}). Epifauna taxon richness is highest in the deep-sea off the shelf in Davis Strait (53 ± 15 taxa; mean ± SD) and lowest in troughs (30 ± 13 taxa). Finally, epifauna biomass and taxon richness vary at even finer spatial scales between individual stations and groups of stations, indicated by significant correlation with MEM19 and MEM20 (distance of ca. 10–50 km; Table B.5). Latitude,

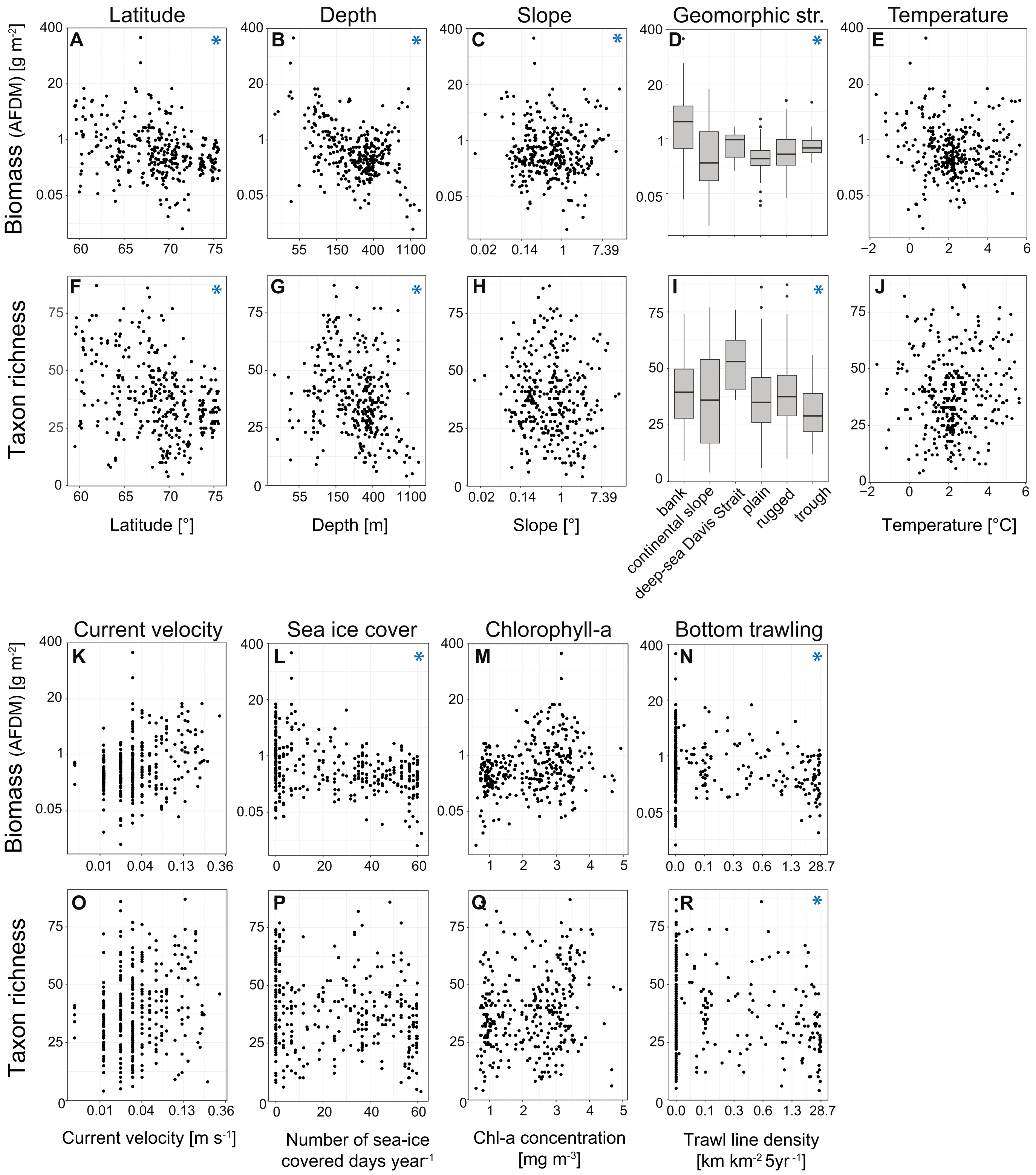

Fig. 3. Effect of environmental drivers on total epifauna biomass (AFDM: ash-free dry mass) and taxon richness. Blue asterisk: environmental driver is a significant predictor of biomass/taxon richness (exact *p*-values available in Table B.5). Note non-linear axes in B, C, G, H, K, O (log-transformed) and N, R (boxcox-transformed). Geomorphic str.: Geomorphic structure.

days of sea-ice cover, depth, geomorphic structures, and bottom trawling are the most important significant drivers of epifauna biomass and taxon richness (Table B.5). All spatial and environmental predictors together explained around 40 % of the variance in biomass and taxon richness.

3.2. *Epifauna community composition*

3.2.1. *Spatial patterns and drivers of epifauna community composition*

Epifauna community composition changes substantially over small distances. While the communities share 50 % of taxa at a distance of <1

Table 2
Effect of environmental and spatial predictors (drivers) on epifauna biomass (AFDM: ash-free dry mass) and taxon richness; results of linear models. '+' indicates a positive, '–' a negative effect; no indication for geomorphology as this is a categorical variable. Numbers give the relative contribution to the overall R^2 of the model (lmg). Listed are only significant predictors ($p < 0.05$, $lmg > 0$). Detailed model results are shown in Table B.5.

Drivers & community characteristics	log(AFDM)		Taxon richness	
Linear model - adjusted R^2:	0.44		0.41	
latitude	–	3	–	9
depth	–	9	–	5
log(slope)	+	2	NA	NA
geomorphology	NA	9	NA	7
days of sea-ice cover	–	7	NA	NA
trawl line density (boxcox-transformed)	–	4	–	5
MEM2	–	1	NA	NA
MEM4	–	2	–	2
MEM6	+	2	+	1
MEM8	+	1	+	1
MEM9	NA	NA	+	1
MEM10	NA –	NA	+	1
MEM11	NA	NA	+	1
MEM12	+	4	+	2
MEM15	+	2	NA	NA
MEM19	NA	NA	–	3
MEM20	NA	NA	–	2

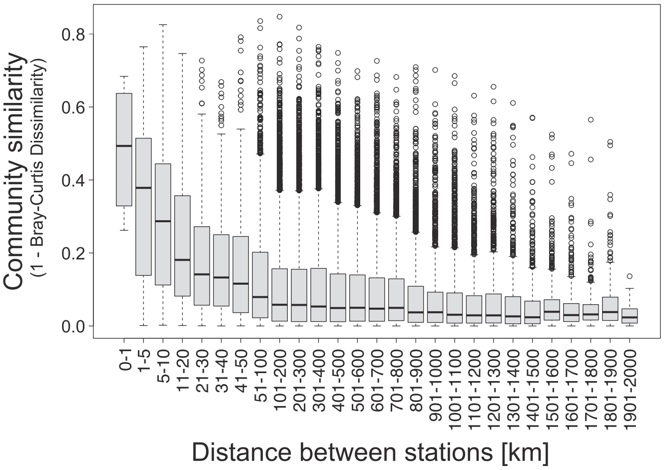

Fig. 4. Similarity of epifauna communities over distance. Similarity is expressed as '1- Bray-Curtis dissimilarity' and decreases with increasing distance.

km, they share only 20 % of taxa at a distance of 11–20 km and < 5 % of taxa at a distance of >101 km (Fig. 4).

Spatial patterns of epifauna community composition are (in parts) shaped by the specific environmental niches of predominant taxonomic groups, given by a combination of latitude, depth, geomorphic structure, temperature, slope, bottom-water current velocity, surface chlorophyll *a*, and trawl line density (Fig. 5B, Table 4, Table B.7). In the south (Labrador Sea, Davis Strait), sponges and sea cucumbers are more often predominant (in AFDM; Fig. 2B, Fig. 5B), with sponges mostly in the deep sea, on the steep continental slope, under relatively high temperature (around 3 °C) and the suspension-feeding sea cucumber *Cucumaria frondosa* on the shallower banks, under low temperature (0–2 °C on average), high surface chlorophyll *a* concentration and/or current velocity. In Baffin Bay, where the continental shelf is deeper (Fig. 1A), anthozoans (anemones, corals), malacostracans (shrimp, crabs), and sea stars are often predominant, particularly on relatively flat plains and in troughs, under average temperatures of 2.1–2.5 °C, relatively low surface chlorophyll *a* concentration and/or relatively low bottom-water current velocity. Epifauna communities differ particularly between (1) deep plains and troughs, (2) the continental slope, and (3) shallow banks (Fig. 5B, Table 4), whereas rugged terrain hosts most community types and therefore shows poor delineation. Due to the high small-scale variability of epibenthic communities (Fig. 4), the environmental drivers and spatial predictors (MEMs) have a limited predictive power (31 % of variability explained by CCA; co-inertia/total inertia).

3.2.2. Epifauna feeding and movement traits

The biomass of sessile, crawling, and filter-feeding taxa decreases from the Labrador Sea over Davis Strait to Baffin Bay, while the biomass of predators and facultative swimmers increases (Fig. 6B, E; Table B.8). At the same time, the biomass of crawlers, filter feeders and predators decreases with depth, while the biomass of deposit feeders increases (Fig. 6A, D). Epifauna communities where filter-feeding taxa predominate (in AFDM) show the highest average taxon richness and high biomass (Table 3).

3.2.3. Davis Strait as biogeographic boundary

Epifauna community composition differs between the Labrador Sea (<62°N) and Baffin Bay (>67°N) (ANOSIM: $p = 0.001$, $R = 0.23$, Table B.9) with Davis Strait (62–67°N) as mixing zone rather than a non-permeable boundary (Fig. 5A). Accordingly, species in Davis Strait are a mix of species from Baffin Bay and the Labrador Sea, with 21 % of species occurring in Davis Strait and Baffin Bay (e.g. the bivalve *Megayoldia thraciaeformis*), 5 % of species occurring in Davis Strait and the Labrador Sea (e.g. the sponge *Geodia barretti*), and 52 % of species occurring in all three seas (e.g. the sponge *Polymastia thielei*; full species list available in Table B.1). Only 17 % of species are limited to Baffin Bay (e.g. the sea star *Icasterias panopla*), 2 % of species are limited to the Labrador Sea (e.g. the sponge *Geodia atlantica*), and 3 % of species are limited to Davis Strait (e.g. the sea urchin *Phormosoma placenta*).

3.3. Impact of bottom trawling

Bottom trawling (bottom trawl line density) is associated with reduced epifauna biomass ($p = 0.0001$) and taxon richness ($p = 2\cdot10^{-6}$) (Fig. 3N, R; Table B.5) and is the fourth-most important driver of epifauna biomass and third-most important driver of taxon richness (Table 2). Accordingly, areas with a high bottom-trawling footprint i.e., the inner Disko Bay and Vaigat, are epibenthic 'coldspots' of low epibenthic biomass and taxon richness (Fig. 2A, C). Particularly sessile and/or filter-feeding taxa have lower biomass under high than under low trawling impact (sessile $p = 0.04$, filter feeder $p = 0.007$, Fig. 6C, F). Bottom trawling had little spatial variation between 2014 and 2018 (Fig. A.5), hence most areas were affected by either high or low high trawl-line density (Fig. 2C).

4. Discussion

With 464 epifauna taxa recorded in the 290,000 km^2 area, the West Greenland continental shelf and slope harbors a diverse and biomass-rich epifauna community, where epifauna diversity is similar to or slightly lower compared to other Arctic regions, while epifauna biomass is similar or slightly higher (Table 5). As hypothesized, benthic epifauna show a high variability on all spatial scales, with differences between latitudes (2000 km), seas (500–1000 km), regions (100–500 km), geomorphic structures (10–100 km), and water depths (30–1400 m). The unexpectedly high spatial variability (Fig. 4) is shaped by strong environmental gradients, such as the duration of the annual sea-ice cover, the distribution of water masses, fronts, marine landscapes and bottom trawling (Fig. 7).

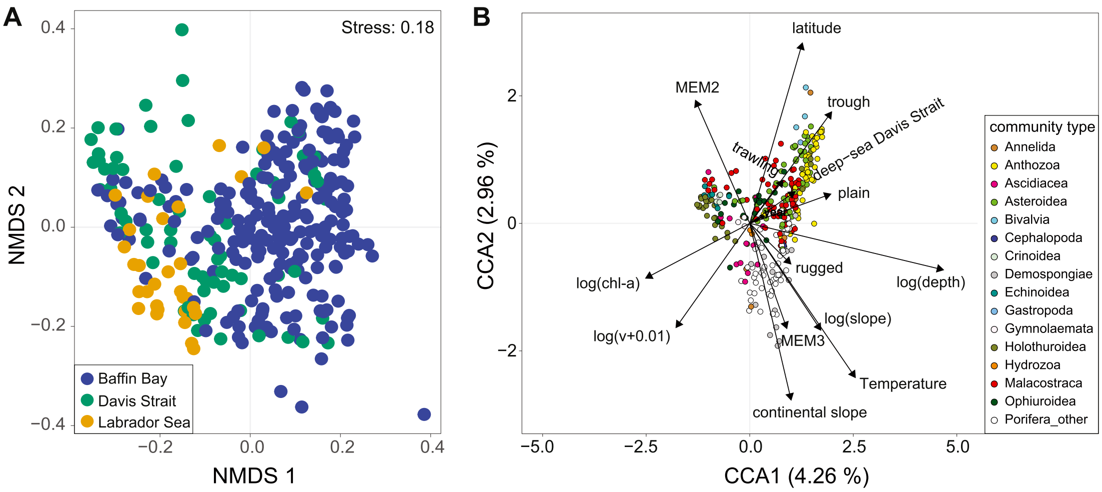

Fig. 5. Epifauna community composition and drivers. A: Non-metric multi-dimensional scaling (NMDS) plot showing differences in community composition (on 'assigned taxon' level, Table B.1) from the Labrador Sea in the south (yellow dots, i.e. stations) to Baffin Bay in the north (blue dots), with Davis Strait (green dots) as 'mixing area'. B: Drivers of epibenthic community composition (community types), derived from constrained correspondence analysis (CCA). Percent numbers in brackets represent the percent variation explained by the respective axis. v: current velocity, chl-a: chlorophyll *a* concentration, trawling: bottom trawl-line density. MEM2-MEM3: spatial predictors representing the scale of different seas (MEM2: highest on Store Hellefiske Bank, MEM3: highest in Southwest Greenland). For better readability, MEM4-MEM37 and sampling year (low effect) are not shown.

4.1. *Latitudinal and depth gradients of biomass: Caused by limited food availability?*

Evidently, epifauna biomass in West Greenland declines with increasing latitude and depth (Fig. 3A, B), but what causes this correlation? Gradients in food availability seem like an obvious explanation, but surface chlorophyll *a* concentration and bottom-water current velocity, proxies of phytoplankton biomass and food transport (Gili and Coma, 1998), were not significant predictors of epifauna biomass in our study. However, a decrease of benthic biomass with increasing depth is a global phenomenon, that is typically attributed to the diminishing downward flux of POM (Rex et al., 2006). Furthermore, the strong, negative effect of sea ice on epifauna biomass (Fig. 3L), especially in Melville Bay (northern Baffin Bay), corroborates the limiting role of food availability and potentially masks a direct effect of surface chlorophyll *a* concentration. The 1–2 month-long sea-ice cover in Melville Bay causes low phytoplankton biomass (low surface chlorophyll *a* concentration, Fig. A.3), likely due to limited under-ice light (Mundy et al., 2014; Oziel et al., 2019) and stronger stratification during the phytoplankton growth season, leading to decreased vertical carbon export (Dybwad et al., 2022). In the Arctic Ocean, a similar decrease of benthic biomass with increasing sea-ice cover was also attributed to food limitation (Degen et al., 2015; Vedenin et al., 2018). Permanently ice-free polynyas, such as the North Water Polynya in northern Baffin Bay, can therefore sustain enhanced phytoplankton productivity, carbon export (Klein et al., 2002; Odate et al., 2002) and benthic biomass compared to ice-covered regions (Roy et al., 2014). Although sea-ice algae have been identified as important food source for polar benthos (Søreide et al., 2010; Yunda-Guarin et al., 2020), their biomass in the Arctic is by far lower than the biomass of phytoplankton (Oziel et al., 2019) and apparently not sufficient to balance the limiting effect of sea ice. Sessile, filter-feeding epifauna show the strongest biomass reduction with increasing latitude (Fig. 6B, E), corresponding to their typically high carbon demand and direct reliance on fresh organic matter from the ocean surface (de Froe et al., 2022; Hanz et al., 2021; Maier et al., 2023).

Surface chlorophyll *a* concentration and bottom-water current velocity may not appropriately reflect food availability at the seafloor for several reasons. Surface chlorophyll *a* concentration was derived from satellite data, which do not account for the subsurface chlorophyll maximum common for the study region (Oziel et al., 2019; Toullec et al., 2021). Grazing, remineralization and lateral displacement of phytoplankton (detritus) by currents influence the POM flux to the seafloor (Lam and Bishop, 2007; Mouw et al., 2016). Direct measurement of the POM flux or sedimentary organic carbon are therefore better predictors for benthic biomass (e.g. Grebmeier et al., 2006), but these measurements were not feasible here. Finally, modeled bottom-water current velocity in our study excludes the influence of tides, that create near-bottom turbulence and resuspension and can substantially enhance food available to benthic ecosystems (Schulz et al., 2021).

4.2. *Biodiversity gradients: Driven by water masses and biogeographic boundaries?*

The observed epifauna biodiversity gradients reflect the broad-scale distribution of water masses in West Greenland (Fig. 1C) and previously proposed biogeographic realms (Costello et al., 2017; Victorero et al., 2023). At Davis Strait (e.g. Store Hellefiske Bank), the co-occurrence of Arctic species from Baffin Bay and Atlantic species from the Labrador Sea locally enhances epifauna taxon richness (Fig. 2A, 3A). Accordingly, Davis Strait, more specifically the area between Fyllas Bank and the Store Hellefiske Bank, is a transition zone (hydrographic front) between polar and Atlantic surface water (Rysgaard et al., 2020). Similar hotspots of benthic biodiversity occur on the Canadian side of Davis Strait (Murillo et al., 2018; Roberts et al., 2021) and at other fronts between Arctic and Atlantic water masses in the Barents Sea and the Chukchi Sea (Jørgensen et al., 2022). Likewise, the observed peak of epifauna taxon richness at ca. 150–250 m water depth (Fig. 3G) coincides with the front between surface and deeper water masses (Hansen et al., 2020; Rysgaard et al., 2020).

Our data indicate that Davis Strait represents a permeable biogeographic boundary for epifauna (Fig. 5A), with half of species occurring in both the Labrador Sea and Baffin Bay. In contrast, simulated larval dispersal of shallow-water benthic invertebrates (<100 m; Krumhansl et al., 2023) and distribution of fish (Jørgensen et al., 2005) describe Davis Strait as biogeographic boundary of low permeability. Dispersal of epifauna species across Davis Strait likely depends on their larval behavior. Most planktonic larvae of marine invertebrates initially have positive buoyancy and float/swim to the upper water column or they are retained within a specific intermediate water mass at pycnoclines associated with hydrographic fronts (Corell et al., 2012; Metaxas, 2001).

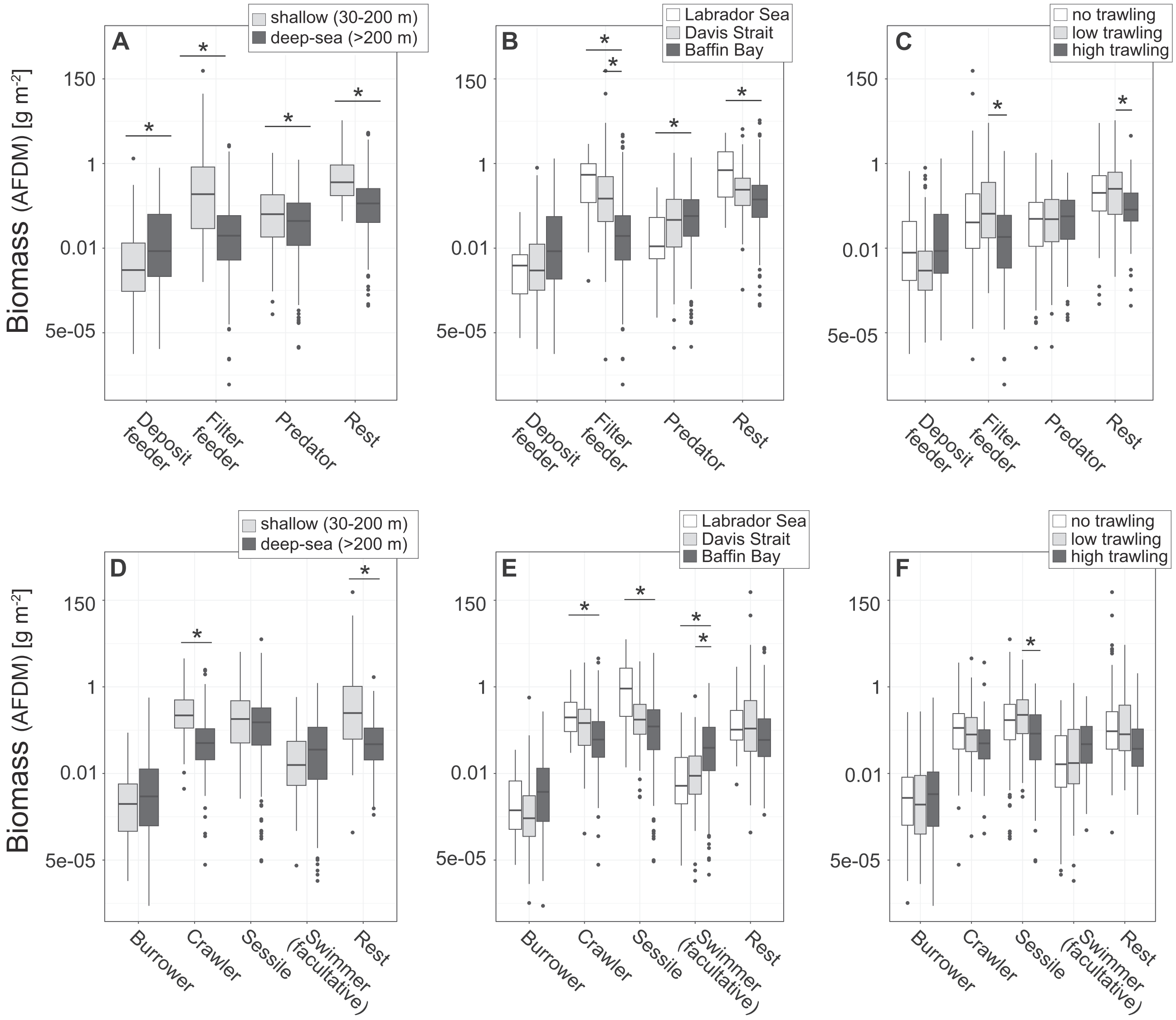

Fig. 6. Biomass of benthic epifauna grouped by feeding traits (upper panel) and movement traits (lower panel) in relation with depth (A, D), sea (B, E) and trawling impact (C, F). 'Rest': taxa with mixed, ambiguous traits grouped. Categories of bottom trawl line density: No trawling (trawl line density 0 km km^{-2} 5 yr^{-1}), low (>0 to <0.6 km km^{-2} 5 yr^{-1}; estimated SAR: >0 to <0.01 km^{2} km^{-2} yr^{-1}) and high trawl line density (0.6–28.7 km km^{-2} 5 yr^{-1}; estimated SAR 0.01–0.6 km^{2} km^{-2} yr^{-1}); note that high trawling intensity refers to the local context, while trawling intensity in other areas (globally) by far exceeds these values (Amoroso et al., 2018). *: significant difference (Dunn test, $p < 0.05$; detailed statistical results and number of replicates are shown in Table B.8).

In West Greenland, larvae drifting in the upper water column are likely retained within the Labrador Sea or Baffin Bay, as surface water masses are separated at Davis Strait (Fig. 1C). However, the surface water front fluctuates interannually between northern and southern Davis Strait (Rysgaard et al., 2020), which could facilitate regular larval transport from one sea to the other. In contrast, larvae that remain in the deep Atlantic Subpolar Mode Water are likely distributed from the Labrador Sea to Baffin Bay (Fig. 1C). Species-specific larval dispersal models could help to explain biogeographic patterns, yet, information on the reproduction and larval behavior of most benthic invertebrates is scarce, especially for deep-sea taxa. Finally, distribution of epifauna taxa depends on larvae settlement and individual growth, which in turn require availability of suitable habitat, as discussed in the following.

4.3. Regional patterns: classifying epifauna habitats

The high variability of epifauna biomass, taxon richness and community composition that we observed in West Greenland between regions (100–500 km; Fig. 2A) and within regions (10–100 km; Fig. 2B, Fig. 4, Fig. 5B) complicates predictive mapping and poses a problem for marine spatial planning. We therefore present a broad classification scheme for initial mapping of benthic habitats and communities in this and other large, understudied regions.

Between-regional differences can be revealed by rough categorization of regions into epifauna 'hotspots' versus 'coldspots' of high versus low biomass and taxon richness (Fig. 2A). The epifauna hotspot on the Store Hellefiske Bank (northern Davis Strait) e.g., might be facilitated by pronounced hydrographic fronts that boost phytoplankton productivity through nutrient upwelling (Munk et al., 2003) and cause species mixing, as outlined in 4.2. Epifauna 'coldspots' in Disko Bay and Vaigat may relate to the high level of disturbance through fishing pressure (Fig. 2C) in areas of high shrimp density e.g., in the northern and southern regions of Disko Bay (Krawczyk et al., 2024), and through intense ice-berg scouring in the area (Krawczyk et al., 2022; Yesson et al., 2017).

Within-region differences of epifauna communities relate (partly) to different geomorphic structures that create unique environmental conditions, described as 'marine landscapes' (Fig. 7) (Al-Hamdani et al., 2007; Harris and Baker, 2012; Ismail et al., 2015). In our study, deep

Table 3

Epifauna community types, characterized by the taxonomic group predominating in biomass (AFDM). Indicated are the number of stations, where a specific community type was found, their total biomass (AFDM) and diversity (taxon richness) (both mean ± standard deviation; highest values underlined), the predominant taxa within each taxonomic group and in brackets the number of stations where those predominate.

Predominant taxonomic group	Common name	Nr of stations	Community biomass (g AFDM m^{-2})	Community diversity (taxon richness)	Predominant taxa
Malacostraca	shrimp, crabs	68	0.5 ± 0.6	31 ± 15	*Pandalus borealis* (52), *Chionocetes opilio* (8), *Hyas coarctacus* (6), *Lithodes* sp. (1), *Pandalus montagui* (1)
Porifera_other	sponges	52	1.5 ± 2.3	47 ± 15	unidentified (48), *Asconema* (4)
Anthozoa	anemones, corals	51	0.6 ± 1.1	36 ± 14	*Actinauge* sp. (32), *Bolocera* sp. (8), *Actinostola* sp. (6), *Pennatula* sp. (2), *Liponema* sp. (2), *Antholoba achates* (1)
Asteroidea	sea stars	49	0.5 ± 0.5	35 ± 18	*Ctenodiscus crispatus* (24), *Hippasteria phrygiana* (8), *Icasterias* sp. (7), *Bathybiaster vexillifer* (3), *Urasterias lincki* (3), *Solaster* sp. (2), *Diplopteraster multiples* (1), *Leptasterias* sp. (1)
Holothuroidea	sea cucumbers	30	13.2 ± 44.7	41 ± 19	*Cucumaria frondosa* (25), *Molpadia* sp. (5)
Ophiuroidea	brittle stars	21	1.2 ± 1.8	38 ± 9	*Ophiura* sp. (13), *Ophiopholis aculeata* (5), *Ophiacantha* sp. (3)
Demospongiae	sponges	15	2.4 ± 4.2	50 ± 14	*Geodia* sp. (6), *Mycale* sp. (4), Axinellida (2), *Haliclona* sp. (1), *Polymastia* sp. (1), Theneidae (1)
Ascidiacea	sea squirts	12	1.3 ± 1.5	49 ± 16	*Kukenthalia* sp. (4), *Ascidia* sp. (3), *Boltenia ovifera* (2), *Dendrodoa* (1), *Synoicum* (1), unidentified (1)
Echinoidea	sea urchins	7	5.1 ± 6	37 ± 11	*Strongylocentrotus* sp. (7)
Annelida	segmented worms	6	1.3 ± 1.1	42 ± 18	all Polychaeta: Onuphidae (2), Polynoidae (1), Sabellida (1), Serpulidae (1), *Spiochaetopterus* sp. (1)
Crinoidea	feather stars	4	6.1 ± 6.6	27 ± 10	*Heliometra glacialis* (4)
Gymnolaemata	moss animals	3	1.4 ± 1.6	48 ± 23	*Alcyonidium* sp. (2), *Carbasea* (1)
Bivalvia	bivalves	3	0.7 ± 0.3	22 ± 1	*Megayoldia* (3)
Hydrozoa	hydrozoans	2	0.3 ± 0	41 ± 12	Sertulariidae (1), unidentified (1)
Cephalopoda	e.g. octopodes	2	0.2 ± 0.1	42 ± 2	Octopoda (2)
Gastropoda	slugs & snails	1	2	31	*Buccinum* sp. (1)

plains plus troughs, the continental slope, and shallow banks show distinct epifauna communities (Fig. 5B, Table 4), similar to marine landscapes in northern Norway (Gonzalez-Mirelis and Buhl-Mortensen, 2015; Mortensen et al., 2009; Silberberger et al., 2019). Shallow banks and a steep continental slope, characteristic of the Greenlandic Labrador Sea (Fig. 1), form complex landscapes of hard/mixed substrate (Gougeon et al., 2017), relatively strong currents (Table B.3), and a hydrodynamic regime that likely promotes high food availability at the seafloor (Bluhm et al., 2020; Schulz et al., 2022). These landscapes facilitate a high biomass of sessile filter-feeding epifauna i.e., sea cucumbers (mostly *Cucumaria frondosa*) on shallow banks and sponges (e.g. *Polymastia* sp., *Asconema* sp., *Geodia* sp.) on the deeper continental slope (Fig. 5B). Similar sponge-dominated ecosystems occur abundantly also on the Canadian continental slope of Baffin Bay, Davis Strait and the Labrador Sea (Dinn et al., 2020; Murillo et al., 2018). In contrast, deep troughs and plains and a more gentle continental slope, typical for the Greenlandic Baffin Bay, form landscapes of soft substrate (Gougeon et al., 2017; Krawczyk et al., 2022), lower current speed (Table B.2), and likely lower food availability, promoting soft-sediment epifauna with mixed feeding modes (deposit feeders, opportunistic feeders, predators) i.e., sea stars, anemones (mostly *Actinauge cristata*), and malacostracans (mostly *Pandalus borealis*, i.e. northern shrimp). Sea stars dominate the biomass in many Arctic regions i.e., parts of the Chukchi Sea (Feder et al., 2005; Rand et al., 2018), Bering Sea (Stevenson and Lauth, 2012), and Beaufort Sea (Rand et al., 2018), probably due to their insensitivity to food limitation (Feder and Christensen, 1966). The high biomass of northern shrimp (*Pandalus borealis*) and its key role in the Arctic ecosystem and for the Greenlandic fishery could be facilitated by its opportunistic diet, ranging from benthic fauna to gelatinous plankton (Berenboim, 1981; Urban et al., 2022; Wienberg, 1980).

The proposed broad classification scheme (Fig. 7) can be used to roughly predict epifauna community types for specific regions and geomorphic structures, but it neglects important small(er)-scale patterns and dynamics of benthic ecosystems (Ingels and Vanreusel, 2013). For instance, features such as seamounts, sills, ridges, and underwater cliffs can provide hard substrate and locally change the hydrodynamic conditions, promoting advection of surface-derived food to the seafloor (Mohn et al., 2023). On an even smaller scale, dropstones amidst soft-substratum also provide a habitat for sessile epifauna in areas otherwise dominated by mobile epifauna and infauna and thereby enhance biodiversity locally (Meyer et al., 2016; Zhulay et al., 2019). Studies focusing on these features and specific regions could help identify patterns of benthic communities at higher spatial resolution (Pearman et al., 2020; Krawczyk et al., 2021b; Meyer et al., 2023).

4.4. Bottom trawling: an important anthropogenic driver

In line with previous studies (Blicher and Hammeken, 2021; Jørgensen et al., 2016; Yesson et al., 2017), we find that bottom trawling reduces epifauna biomass and taxon richness, especially of sessile and/or filter-feeding taxa like sponges and corals that form vulnerable marine ecosystems (VMEs; United Nations General Assembly Resolution 61/105, 2007) e.g., glass sponge communities or sea pen fields in the study area (Table B.1). In fact, comparison with natural environmental factors reveals that bottom trawling is one of the strongest epifauna drivers in the area (Table 2) and seems to promote epifauna coldspots (e.g. in inner Disko Bay), which has not been documented before. At the same time, our data and other studies (Beazley et al., 2013; Hanz et al., 2022; Kutti et al., 2013) demonstrate the important contribution of filter-feeding epifauna to total benthic biodiversity, biomass and metabolic activity. Loss of these likely impairs benthic ecosystem functioning e.g., benthic carbon storage, seawater filtration, organic matter remineralization and nutrient regeneration (Pham et al., 2019). However, the effect of bottom-trawling on benthic ecosystem functioning remains ambiguous (Epstein et al., 2022). So far, trawling-related shifts of benthic biogeochemistry have been attributed mostly to sediment reworking (van de Velde et al., 2018), removal of organic carbon and bioturbating fauna (De Borger et al., 2021), and changes in microbial diversity (Bonthond et al., 2023), while the role of epifauna has been neglected.

Since 1950, the majority of the West Greenland shelf has been trawled over at some point (Blicher and Hammeken, 2021; Yesson et al., 2017). However, over the study period and in the recent years, trawling areas in West Greenland have remained relatively stable (Fig. A.5) and

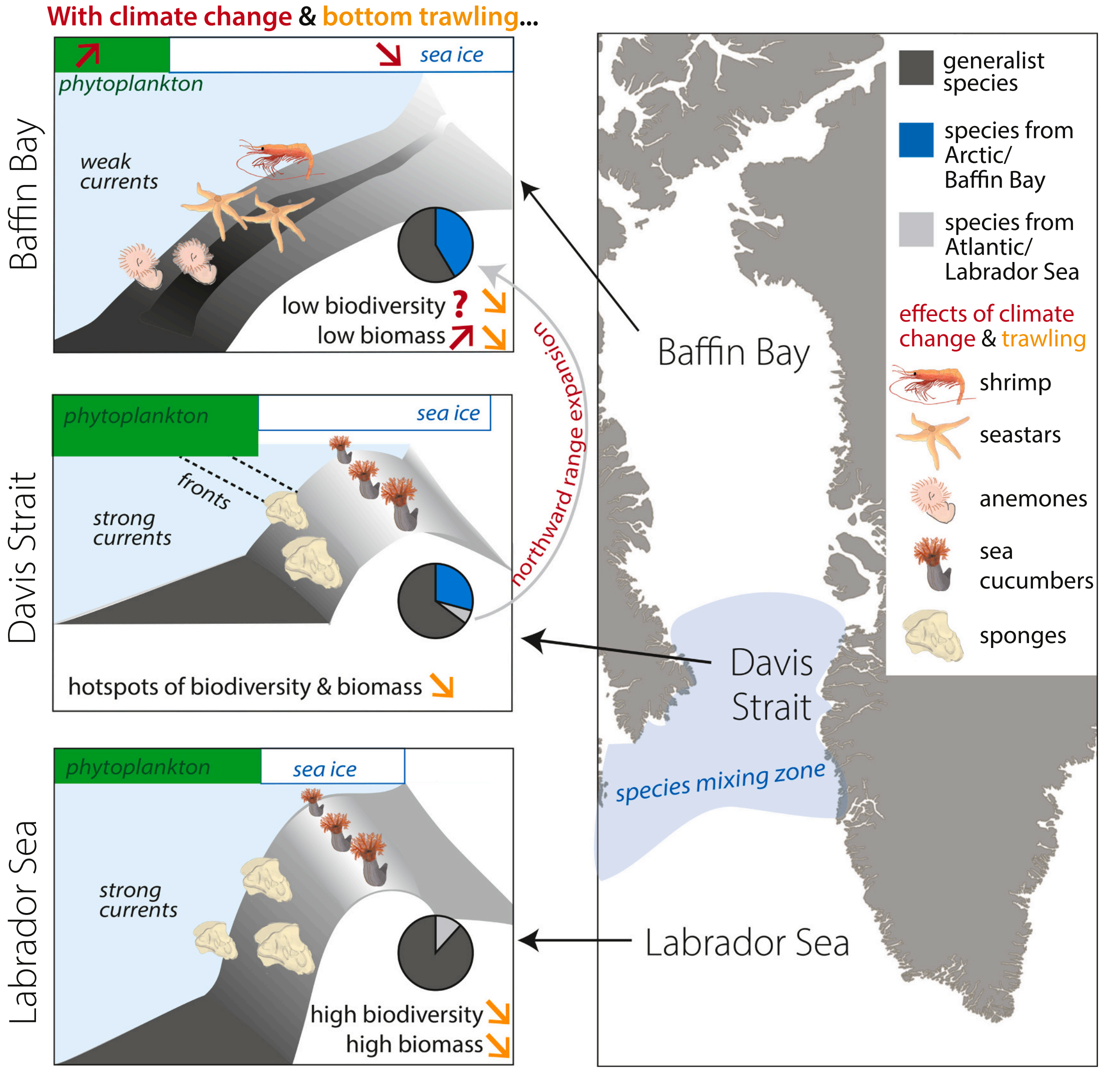

Fig. 7. Simplified patterns of benthic communities in Baffin Bay, Davis Strait and the Labrador Sea, in relation to the area-specific environment. Pie chart: species composition, i.e. species limited to Atlantic water masses in the Labrador Sea (light grey), species limited to Arctic water masses in Baffin Bay (blue) and generalist species occurring in both water masses (dark grey). In red: hypothesized effects of climate change, in orange: measured effects of bottom-trawling fisheries.

substantial northward expansion of fisheries, as seen in other regions (Christiansen et al., 2014), has so far not been profitable (Burmeister and Buch, 2023; Nogueira and Hedges, 2023). Given the high spatial variability of epifauna and the strong impact of trawling, particularly at the first hit (Morrison et al., 2020), continuation of this 'footprint-freeze', where fishing efforts are limited to already impacted areas (Long et al., 2021), seems most beneficial to maintain benthic ecosystems and their important function in this sensitive region.

4.5. *Conclusions and implications under climate change*

Based on an extensive, unprecedented data set, we demonstrate the previously unknown variability of epibenthic communities in West Greenland and identify patterns of their large-scale and regional distribution. These findings allow us to depict a possible response of benthic communities to the rapidly-changing climate in the Arctic (Rantanen et al., 2022) and to bottom-trawling fisheries (Fig. 7). As epibenthic communities in Eastern Baffin Bay are currently limited by the duration of sea-ice cover, the rapidly decreasing sea-ice cover and the resulting increase in phytoplankton productivity (Krawczyk et al., 2021a; York et al., 2020) should boost secondary benthic production and biomass. On Antarctic shelves, benthic biomass is estimated to store an annual extra of 2.9 million tons of carbon due to decreasing sea-ice cover (Barnes, 2015). However, increased benthic biomass and carbon storage potential remain ambiguous. In the Arctic, an increase of phytoplankton production might be limited by nutrient availability and enhanced cloud cover due do climate change (Bélanger et al., 2013; Walsh et al., 2005). Export of phytoplankton biomass could be restrained by pelagic consumption, increased stratification, and changes in phytoplankton taxonomic composition (Ardyna et al., 2020; Ardyna and Arrigo, 2020), which can be very different from the Antarctic. Finally, not all benthic communities and regions may benefit equally. In the Bering Strait, both positive and negative trends in benthic biomass have been documented, depending on the predominant species and regional differences in (changing) hydrodynamics and sea ice (Grebmeier et al., 2018). Our results indicate that increased food supply in Baffin Bay could particularly benefit high-biomass filter-feeding epifauna. Some studies propose that over the last century, the inflow of polar water from the Arctic Ocean to Baffin Bay decreased, while the inflow of Atlantic Subpolar Mode Water increased (Grivault et al., 2017; Zweng and Münchow, 2006). This could facilitate a northward range expansion of Atlantic species, e.g. filter-feeding sponges, into the Arctic (Renaud et al., 2015). However, it appears unlikely that the future Baffin Bay will host sessile filter feeders at the same density as the Labrador Sea, because the deeper

Table 4

Environmental niches of community types, given as mean ± standard deviation of environmental parameter at the stations, where the community types were found. Geomorphic structures are presented in ranked order, with number of stations in brackets.

Community type	Latitude (°N)	Depth (m)	Slope (°)	Temperature (°C)	Current velocity (m s^{-1})	Chlorophyll a (mg m^{-3})	Trawl line density (km km^{-2} 5 yr^{-1})	Geomorphic structures
Malacostraca	69 ± 4	269 ± 110	1.0 ± 1.2	2.5 ± 0.9	0.05 ± 0.05	2.0 ± 0.9	2.1 ± 3.7	rugged (40) plain (20) bank (6) cont. Slope (1) deep sea (1)
Porifera_other	67 ± 5	338 ± 189	2.0 ± 2.3	2.9 ± 1.4	0.05 ± 0.04	2.3 ± 1.0	1.5 ± 4	rugged (27) cont. Slope (13) plain (10) deep sea (1) trough (1)
Anthozoa	71 ± 3	488 ± 167	1.3 ± 2.2	2.5 ± 1.0	0.02 ± 0.02	1.5 ± 0.8	0.9 ± 2.6	plain (20) rugged (13) trough (8) cont. Slope (6) deep sea (4)
Asteroidea	69 ± 3	391 ± 266	1.1 ± 1.5	2.1 ± 1.6	0.04 ± 0.03	2.3 ± 1.1	0.5 ± 1.3	rugged (22) plain (14) trough (8) cont. Slope (4) bank (1)
Holothuroidea	66 ± 3	239 ± 351	0.8 ± 1.0	1.3 ± 1.2	0.07 ± 0.06	2.6 ± 0.9	1.3 ± 4.1	bank (19) rugged (6) cont. Slope (5)
Ophiuroidea	70 ± 5	172 ± 89	0.7 ± 1.0	1.5 ± 1.2	0.03 ± 0.03	2.0 ± 1.1	0.5 ± 1.8	rugged (14) bank (7)
Demospongiae	66 ± 4	364 ± 237	2.5 ± 4.8	3.3 ± 1.7	0.06 ± 0.08	2.4 ± 0.9	0.1 ± 0.3	rugged (7) cont. Slope (6) deep sea (1) plain (1)
Ascidiacea	66 ± 5	142 ± 56	1.0 ± 0.9	2.2 ± 1.6	0.08 ± 0.06	3.0 ± 0.9	0.6 ± 1.0	rugged (9) bank (2) plain (1)
Echinoidea	67 ± 2	88 ± 17	0.4 ± 0.2	0.2 ± 1.4	0.1 ± 0.09	2.6 ± 0.6	0 ± 0	bank (6) rugged (1)
Annelida	67 ± 6	232 ± 140	0.7 ± 0.4	2.6 ± 0.8	0.07 ± 0.07	2.1 ± 0.9	2.0 ± 4.3	plain (4) bank (1) rugged (1)
Crinoidea	70 ± 1	97 ± 8	1.1 ± 1.4	−0.3 ± 1.0	0.03 ± 0.01	2.9 ± 0.4	0.1 ± 0.2	bank (2) rugged (2)
Gymnolaemata	66 ± 1	173 ± 86	1.0 ± 0.8	2.4 ± 1.3	0.09 ± 0.01	2.7 ± 0.6	1 ± 1.4	rugged (2) slope (1)
Bivalvia	70 ± 3	423 ± 95	0.9 ± 0.3	2.3 ± 0.2	0.03 ± 0.03	3.1 ± 0.2	10.9 ± 15.5	plain (2) trough (1)
Hydrozoa	70 ± 1	303 ± 87	1.2 ± 1.4	2.3 ± 0.2	0.03 ± 0.01	4.1 ± 0.9	2.2 ± 1.9	plain (1) rugged (1)
Cephalopoda	71 ± 5	350 ± 24	0.9 ± 0.6	2.3 ± 0.6	0.05 ± 0.04	1.7 ± 1.0	0.1 ± 0	slope (1) rugged (1)
Gastropoda	71	393	0.5	2.9	0.04	3.0	0	trough (1)

Table 5

Biodiversity (taxon richness) and biomass of epibenthos in different Arctic regions. Only trawl data are included in this comparison; however, differences in methodology (e.g. trawl gear, duration) complicate comparability.

Region	Biodiversity	Biomass	Reference
West Greenland (Baffin Bay, Davis Strait, Labrador Sea; total area ca. 325,000 km^2)	4–87 taxa per 250–3500 m^2 473 taxa in total	0.01–242 g AFDM m^{-2} 0.1–1549 g WM m^{-2}	Present study
Arctic Ocean	20–30 taxa per 200–5000 m^2	0.03–643 g WM m^{-2}	(Carey, 1991; MacDonald et al., 2010; Zhulay et al., 2019)
Canadian Baffin Bay & Beaufort Sea	16–374 taxa per 1000 m^2 527 taxa in total	<1–77 g WM m^{-2}	(Roy et al., 2014)
North East Greenland	8–66 taxa per 9600–21,000 m^2 276 taxa in total	2–11 g AFDM m^{-2} 65–528 g WM m^{-2}	(Fredriksen et al., 2020; Piepenburg and Schmid, 1996)

shelf and more gentle continental slope of Baffin Bay do not provide enough suitable habitat (Fig. 7). Even if filter-feeding epifauna of high biomass should expand, their ability to store carbon and act as climate mitigation remains questionable, as these benthic hotspots are often net CO_2 sources due to their high metabolic activity. Commercial bottom-trawling limits epifauna throughout the study area as it reduces epifauna biomass and taxon richness and appears of similar importance as driver of benthic communities compared to natural environmental gradients. To investigate the fate of Arctic epibenthos, time series in different Arctic regions should be established to closely monitor shifts in benthic community biomass, biodiversity and carbon cycling.

CRediT authorship contribution statement

Sandra R. Maier: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Nanette Hammeken Arboe:** Writing – review & editing, Methodology, Investigation, Data curation. **Henrik Christiansen:** Writing – review & editing, Formal analysis, Data curation. **Diana W. Krawczyk:** Writing – review & editing, Formal analysis, Data curation. **Lorenz Meire:** Writing – review & editing, Formal analysis, Data curation. **John Mortensen:** Writing – review & editing, Formal analysis, Data curation. **Koen Planken:** Writing – review & editing, Formal analysis, Data curation. **Kirstin Schulz:** Writing – review & editing, Formal analysis, Data curation. **Anna-Selma van der Kaaden:** Writing – review & editing, Formal analysis, Data curation. **Tobias Reiner Vonnahme:** Writing – review & editing, Formal analysis, Data curation. **Nadescha Zwerschke:** Writing – review & editing, Project administration, Formal analysis, Data curation. **Martin Blicher:** Writing – review & editing, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

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.

Data availability

A full list of recorded taxa is provided as Table B.1. Station biomass, biodiversity, community type, environmental and spatial drivers are provided as Table B.3. Code for statistical computing and all supplemental files are available under https://zenodo.org/records/12775491. Georeferenced species data are used directly in the advice to the Government of Greenland on seabed management; these data can only be utilized with permission of the researchers from the Grønlands Naturinstitut. Commercial bottom-trawl logbook data are property of the Greenland Fisheries License Control Authority (GFLK) and confidential due to client protection.

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Appendix A. Supplementary data

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