

Benthic macrobenthos communities on the North-East Greenland Shelf are sparse but biodiverse and linked to the overlaying water mass

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Research Article

Keywords: Arctic, Northeast Greenland Shelf, Benthos, water mass, Biodiversity, Community structure

Posted Date: September 9th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-10807347/v1>

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Additional Declarations: No competing interests reported.

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Abstract: The benthic marine macrofauna communities play a key role in the functioning of marine ecosystems and contribute the majority of species to overall marine biodiversity. The biomass and richness of the macrofaunal community are related to the input of organic matter and therefore distribution of primary production. The linkage between pelagic primary production and benthic secondary production is evident on Greenland continental shelves, due to high productivity and relative shallowness, this close coupling sustains rich fisheries on the west Greenland shelves. This study collected benthic macrofauna grabs, images and cores from 21 stations between August-September 2017 on the North-East Greenland shelf between 74° N and 78° N and found macrofauna abundance 7 times lower than West Greenland shelves, and biomass 30 times lower but similar or larger gamma (ecosystem) diversity. The North-East Greenland shelf is the exception to most continental shelves likely due to low primary production and sedimentary input of organic material resulting in relatively sparse, diverse and pristine macrofauna communities. This continental shelf hosts a highly heterogeneous benthic community on a homogenous seabed, likely influenced by overlaying water masses including the introduction of water masses from an Atlantic origin.

Keywords: Arctic | Northeast Greenland Shelf | Benthos | water mass | Biodiversity | Community structure

Statements and Declarations

I declare that the authors have no competing interests as defined by Springer, or other interests that might be perceived to influence the results and/or discussion reported in this paper.

Funding Declaration

Funding for this research was provided by the Joint Northeast Greenland Strategic Environmental Study Program 2016-2019 and the Horizon Europe Project: Polar Ocean Mitigation Potential (101136875).

Ethics and Consent to Participate: not applicable

Acknowledgements

This study forms part of Joint Northeast Greenland Strategic Environmental Study Program 2016-2019. The Northeast Greenland Environmental Study Programme is a collaboration between DCE – Danish Centre for Environment and Energy at Aarhus University, the Greenland Institute of Natural Resources, and the Environmental Agency for Mineral Resource Activities of the Government of Greenland. We would like to thank the captain and crew on the NEG-2017 Dana R/V cruise.

Introduction

The Northeast Greenland (NEG) shelf is an Arctic shelf located between Greenland and Fram the Strait and stretching between 70 and 82 N, the shelf extents 300 km seaward (Arndt et al. 2015) with relatively shallow angle of bathymetry (Jakobsson et al. 2012) (Fig. 1). The shallow angle results in a broad, shallow continental shelf, with its broadest section of the Greenland margin, ca. 232,000 km² and a shallow shelf with an average depth ca. 230 - 300 m (León et al. 2025).

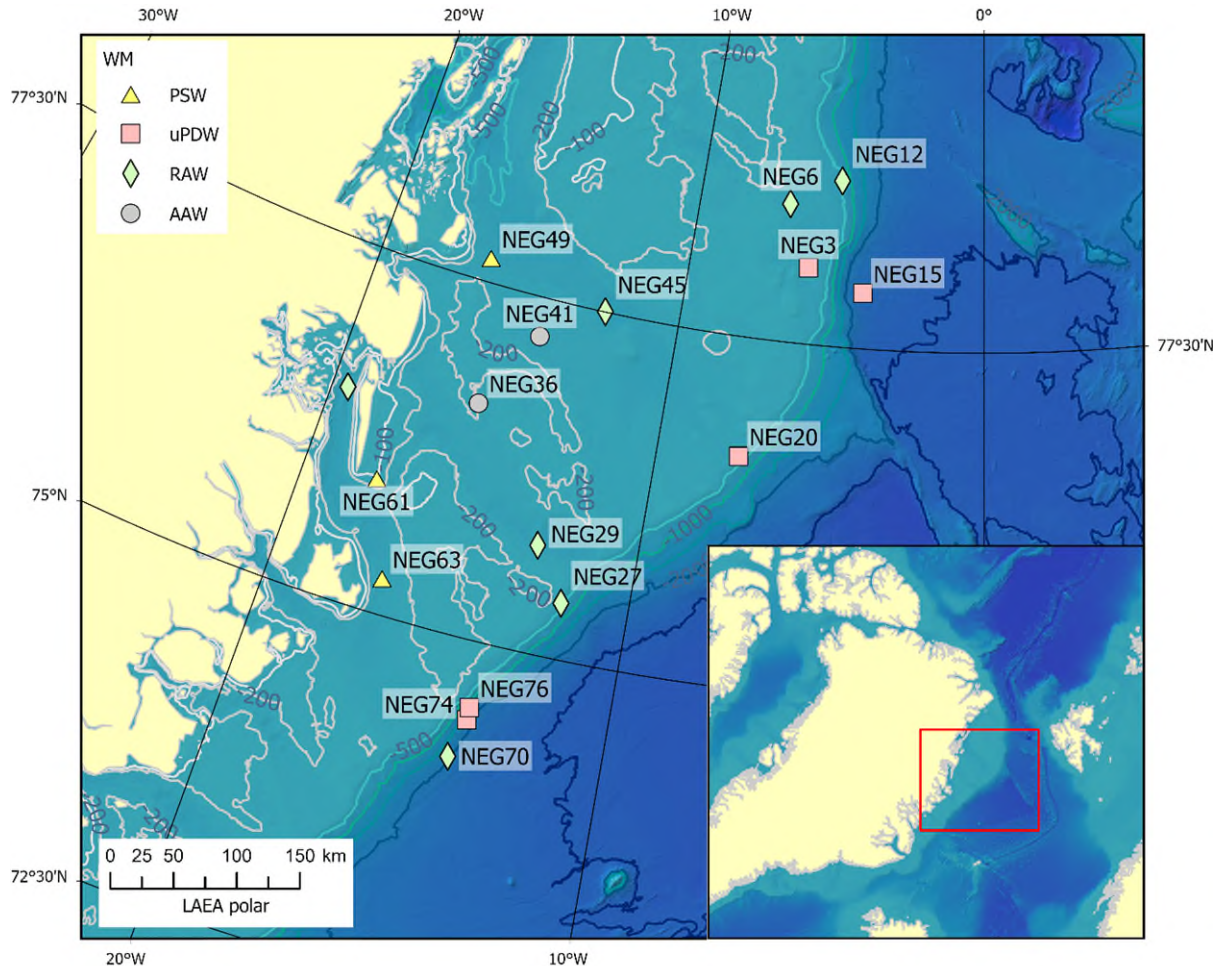


Fig. 1 Map of sampling stations during the NEG-cruise on the R/V Dana during August-September 2017. Water masses (WM) derived from from on major ocean currents and bathymetry, with map bathymetry sourced from Jakobsson et al. (2024).

The NEG shelf is the principal gateway for sea ice export from the Arctic Ocean, and a key feature of the shelf is dominance of cold, low saline surface water, below this cold surface water, is warmer more saline water which originates from Atlantic water being transported north in the eastern Fram Strait (Kwok and Cunningham 2012). The combination of extended sea ice cover, summer stratification and low nitrate content of the surface water results in a very low-productive system with modelled annual production of $\sim 10 - 40 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Vernet et al. 2021).

The Arctic the shelf is changing rapidly in response to climate change with the coastal region is impacted by increased input of glacial ice and meltwater from the Greenland Ice Sheet and decreasing sea ice cover (Stroeve et al. 2012). A further change is the new feature of the NEG is Northeast polynya close to the Belgica Bank

(Starmans et al. 1999), likely a factor in the high epifaunal abundance and biomass at Belgica Bank (Fredriksen et al. 2020) and key area to investigate seafloor biodiversity in pristine habitats.

On the shelf, sea ice cover has decreased (Asbjørnsen et al. 2020) and the distribution of the two main water masses has changed so that the depth of the 0 °C isoline, marking the boundary between the warm and cold-water masses, has moved upward from about 300 m depth to around 150 m depths over a period of 80 years (Gjelstrup et al. 2022). In addition, to this redistribution the deeper warm water has warmed by approximately 1C while the surface water has become less saline. The combination of loss of sea ice and increased inflow of water of Atlantic origin (Arctic Atlantic Water and Return Atlantic Water) has caused a substantial change in the shelf and fjord ecosystem in SE Greenland with shift in the dominant fish and marine mammals (Heide-Jørgensen et al. 2023). Although similar changes in sea ice and distribution of water masses have occurred on the NE Greenland shelf there are limited knowledge of the benthic ecosystem response to these changes.

The benthic marine macrofauna communities play a key role in the functioning of marine ecosystems and contribute the majority of species to overall marine biodiversity. The Arctic benthic marine invertebrates tend to be slow growing and long lived with limited mobility (Grebmeier et al. 2015) making them sensitive to and thus an appropriate integrative indicator of disturbance and human activity in general in an area (Christiansen 2017). Increased human impact and potential vulnerability of benthic communities necessitate the introduction of effective conservation measures and therefore requiring setting baselines and addressing knowledge gaps within NEG shelf.

Across NEG the extensive sea-ice has limited accessibility of the areas for scientific exploration of the shelf seafloor and so far, studies on the NEG benthos have been limited and mostly focused on the open-water polynyas. A number of R/V Polarstern cruises (ARK VII, VIII, IX and X) have covered parts of the area. Further studies Mayer and Piepenburg (1996) and Schnack (1998) conducted studies across the shelf break around 75°, with the area further north, 78° N covered by additional studies (Brandt 1995; Piepenburg and Schmid 1996a; Piepenburg and Schmid 1996b; Schnack 1998). This would be the first study of macrobenthos describing the benthos between 75° N and 78° N, with megabenthic communities addressed by Fredriksen et al. (2020).

In shallow waters, where the productive surface layers are in direct contact with the seafloor, the benthic macrofauna are expected to directly filter suspended phytoplankton and potentially control phytoplankton production if the water column is fully mixed. In deeper waters below the photic zone, benthic communities production is almost exclusively fuelled by allochthonous organic material, sinking from primary production in the photic zone (Carmack and Wassmann 2006), from which often sustain higher trophic levels such as fish, mammals and birds (Bluhm and Gradinger 2008). Due to the pelagic-benthic coupling through sedimentation of phytodetritus standing benthic biomass often mirror the spatial distribution of pelagic productivity, even under small-scale hydrographic features such as productive fronts (Josefson and Conley 1997; Josefson and Hansen 2003).

As the water depth increases, there is loss of labile organic matter through respiration into refractory organic matter (lower degradability) reducing the input of organic matter to the benthos (Bendtsen et al. 2015).

Therefore, the high productivity and relative shallowness of the Greenland continental shelves generally receive a

high input of organic matter supporting an abundant benthic community (Piepenburg and Schmid 1996a) which sustains rich fisheries across the shelf areas (Vernet et al. 2021).

The water masses overlying the NEG shelf are currently dominated by the cold East Greenland Current and a layer of polar surface water on top that carries the largest export of sea-ice out of the Arctic Ocean (Aagaard and Coachman 1968; Carmack and Wassmann 2006; Codispoti et al. 2013; Michel et al. 2015). Below this cold water, Atlantic water is dominating and as the border between the two water masses tend to ascend (Gjelstrup et al. 2022), with more of the shelf seafloor covered with this water and this could potentially affect distributions of benthic communities through changes in dispersal patterns and connectivity (Vernet et al. 2021).

Primary productivity is limited by the extensive sea-ice cover, offshore pack ice for > 10 months a year (Christiansen et al. 2016) which, in combination with low nutrient concentration in the surface layer lead to the low export production to seafloor (Hobson et al. 1995) which in turn, limit benthic fauna production, biomass, abundance and change community composition of the benthic macrofauna and propagate effects to higher trophic levels in the region. A re-distribution of water masses on the NEG could also change and affect the distribution of sedimentary input rates of organic material to the benthic communities on the north-east Greenland Shelves.

The seafloor on North-East Greenland shelf has for long been one of the most remote and inaccessible places on Earth due to the extensive sea ice cover and it is only the open-water polynya which have been subjected to recurrent scientific investigations of the seafloor biodiversity. Therefore, this area is most promising place to look for pristine seafloor habitats and communities as most shelves world-wide have been subjected to intensive trawling activities for many decades. However, the ice cover has already declined and is projected to decline further, and this will increase accessibility and could expose the NEG-shelf for exploitation of raw materials and fisheries. Future protection therefore relies on timely setting of baseline for the seafloor biodiversity. In this study we report benthic sampling of 21 stations on the NEG shelf from the NEG 2017 cruise, is complementary to previous benthic sampling programmes and data collection found in the literature (Heegaard 1941; Bluhm and Gradinger 2008)

Methods

Study Area

During the NEG-cruise on the R/V Dana, 21 stations on the NEG shelf were sampled between August-September 2017. The stations were located between 74° N and 79° N latitude and from 66 to 1,460 m depth, with 14 stations located on the shelf and 7 on the eastern marginal slopes of the shelf (Fig. 1). The overlaying water masses were assigned to major ocean currents based on depth and location on the continental shelf as mapped in Møller et al. (2019). Sampling of the benthic fauna and sediment used a combination of 0.1 m² van Veen grabs, 0.0143 m² Haps-corer (Kannevorff and Nicolaisen 1972) and seafloor photography and video samples. Each sampling station comprised of three Van Veen grabs or five Haps-cores. In total the study comprised 76 van Veen samples and 5 Haps samples, and in total covered 7.6 m² seafloor. 19 of the stations were also surveyed with video and photo recordings before sampling of the fauna (5-15 minutes drifting). Sediment data was retrieved from the surface sediment of the van Veen grabs and 11 Haps samples provided data on sediment chemistry across a 0 – 20 cm sediment depth profile. Additionally, sediment samples collected

in August 2016 by Volcanic Basin Petroleum Research AS were analysed for biomass and sediment organic content (ignition loss).

Sediment samples

Sediment samples water content measured by weighed mass change before and after drying at 105 °C for 24hrs, afterwards ignition loss mass was measured by burning the dried sediment at 470 °C until weighed mass no longer changes. Dried and burned sediment was stored in desiccator, until weighed. Biomass (organic) sediment content was then calculated as dry sediment mass subtracted by ignition loss dry weight sediment.

Macrofauna Samples

Quantitative fauna samples from Van Veen grabs and Haps-corer were sieved through a 1 mm. sieved on board and preserved with 4 % formaldehyde, with additional samples containing sediment preserved in 70% ethanol. All fauna samples were analysed under microscope (10 - 40 x magnification), with animals determined to the lowest possible taxonomic resolution following procedures described in (Hansen and Josefson 2019), and similar to the OSPAR-guidelines (OSPAR 2012).

Video and Seafloor Imaging

GoPro® cameras were mounted on Haps-corer frame, which was carefully lowered to the seafloor and then lifted allowed to ~ 1 m above the seafloor and allowed to drift with the vessel for 1-5 minutes. Once lowered to the seafloor, quantitative still photos were obtained and density counts of epifauna recorded, with qualitative observations of epifauna including bottom-dwelling fish obtained for the drifting video recordings.

Multivariate analysis

Multivariate analysis was conducted with on benthic community using data from photos and Van Veen grabs which had sufficient degrees of freedom for multivariate analysis. Analysis used Primer v7 software all data was transformed with a square root function to prevent the signal of highly abundance species from dominating the results. All data was analysed using a bray-Curtis matrix, followed by a two-way ANOSIM test on the epifauna data (image) investigating water mass and sediment type as factors with associated pair-wise test. Infauna data (van veen grab) was tested using a one-way ANOSIM with water mass as the factor of sediment could not be separated from water mass. Significant differences were investigated using the SIMPER procedure and displayed using nMDS.

Results

Sediment characteristics

All stations consisted of a fine mud (< 0.063 mm grain size) (Folk et al. 1970), this sediment was well sorted and with little variation between samples. The average water content was 26.6 ± 7 %, with average biomass (organic content) at 2.8 ± 0.5 %. The sediment profile did not show any clear trends of water content or biomass change with sediment depth at any stations (Fig. 2). Sediments from depths below 800 m had a brownish colouration with a high degree of foraminifera shells.

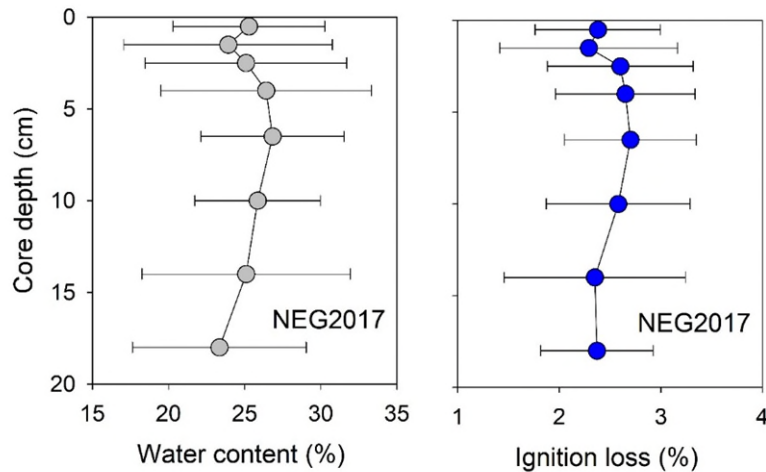


Fig. 2 Sediment profiles of water content (left) and ignition loss (right) shown as average for the 11 stations sampled with Haps corers. Error bars show standard deviation.

The majority of video recordings displayed featureless clay (mud) seafloor which was almost completely covered with pebbles (1-10 cm). In contrast, Van Veen grabs recovered relatively few stones within the sample when compared to the video recordings. At station 49, depth 117 m video recordings revealed scour marks and craters of several meters' depth. These were characteristic of a recent iceberg scour, where the keel of icebergs contacts the seafloor, gouging trenches and craters into the soft sediment (Gutt et al. 1996).

Macrofauna communities

Biomasses ranged between < 0.1 and $63 \text{ g wet weight m}^{-2}$ across the shelf, except for two stations on the NEG continental slopes (St. 76B and 76D), had biomasses up to $2,000 \text{ g wet weight m}^{-2}$, these outliers were removed from all subsequent analysis. In total 298 difference species or taxa (specimens only possible to identify to a high taxonomic level) were identified, with the most species rich phyla were annelids (88 taxa), arthropods (71 taxa), bryozoans (35 taxa), molluscs (30 taxa), echinoderms (23 taxa), cnidarians (20 taxa), porifera (15 taxa) and the other 8 phyla containing 16 taxa.

Average Van Veen samples contained 19 species with all Van Veen grabs ranging between 6 – 30 species, resulting in an average Shannon diversity index of 3.54, with rarefaction estimates revealed for every 20 individuals there is an expected average of 11.4 species (range 5-14). Species richness and diversity showed no clear relation to water depth or sample location. Beta-diversity was assessed as the average richness within randomly accumulated replicates at the same station (total sample area 0.5 m^2). The total station richness (beta-diversity) was 49 species per station and the corresponding Shannon diversity index at 4.61.

32 different taxa were recorded (determined to at least family) with 8 phyla were recorded across 4 water masses, with PSW (Polar Surface Waters) hosting the highest abundance (av. 5.13 ind. m^{-2}), the majority of these in phylum Echinodermata (av. 4.27 ind. m^{-2}). AAW (Arctic Atlantic Water) was dominated by phylum Bryozoa across all station, however the RAW (Return Atlantic Waters) had a high abundance of phylum Annelida, in 3 of 5 stations, with the other 3 stations each being dominated by Bryozoa or Echinodermata and Bryozoa respectively. uPDW (upper Polar Deep Water) had an overall lower abundance (av. 0.91 ind. m^{-2}), with an even distribution across most phylum.

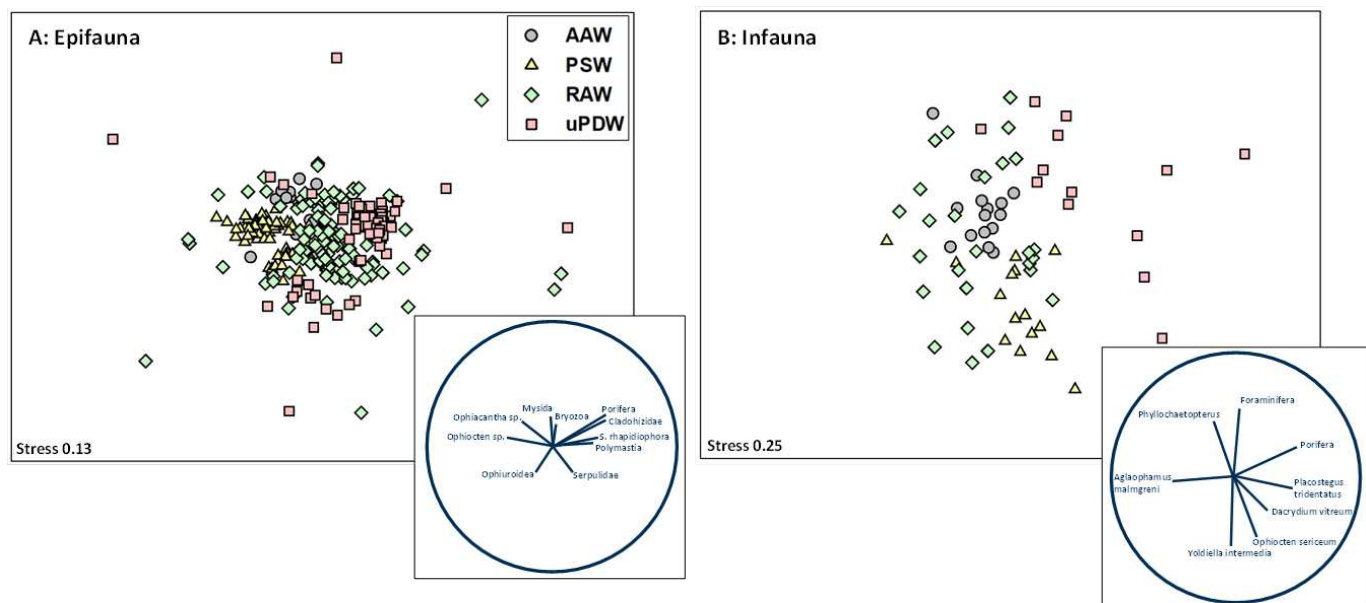


Fig. 3 Benthic community similarities of A: Epifauna and B: Infauna from North-East Greenland (NEG) continental shelf across water-masses from imagery (video stills) and Van Veen grabs respectively, both nMDS plots are based on square-root transformed taxa abundance. nMDS plots were constructed from Bray-Curtis similarity Indices between all samples, with 999 restarts. Inserts describe selected relative vectors (taxa), with values derived from Pearson correlation.

Multivariate ANOISM revealed a significant difference between the benthic community dependent on the water mass, with pairwise test detecting all water masses were distinct from each other with the exception of AAW and RAW (Table 1). These results repeat both epifauna (image) and infauna (van veen grab) samples with sediment was also a significant factor across all sediment types (Fig. 3). SIMPER results identified that RAW had a relatively low av. intra-group similarity, 15.30 when compared across all water masses with groups such as Serpulidae, Bryozoa and Ophiuroidea key in distinguishing the benthic communities (Supplemental materials).

Observation of *Umbellula encrinus* (giant sea pen) were also found during the survey these individuals were estimated to be approximately 45 years old using annual growth rings (+30 growth rings) and growth rates (> 200 cm height / 4.5 cm yr⁻¹). (Could we add photograph in-situ of species and/or rings?).

The NEG survey predicted species richness for arthropods and annelids at 100 individuals (rarefaction₁₀₀) at 32.4 which was higher than any observed West Greenland continental shelf investigation (Fig. 1.) and with steeper species accumulation curves, with data including fjords, banks and shelf plain (Fig. 4), indicating a higher beta and gamma-diversity. “Chao₂” – estimates (Chao 1984), of the Kanumas-investigation located in fjords, banks and shelf plains along the West Greenland shelf gave the highest arthropods and annelids species richness (262), followed by the NEG 2017 investigation (217 records). However, the rate of increase going from the last two stations (18 to 19) was highest for the NEG 2017 survey (addition of 5.61 species).

	Epifauna		Infauna		211
	R Statistic	P-Value (%)	R Statistic	P-Value (%)	212
Global Tests					213
Water mass (WM)	0.450	0.1	0.249	0.1	214
Sediment (Sed.)	0.408	0.1	-	-	
WM Pairwise Tests					215
RAW - uPDW	0.484	0.1	0.395	0.1	216
RAW - AAW	-0.082	81.8	-0.082	94.9	217
RAW - PSW	0.225	0.1	0.176	0.7	
uPDW - AAW	0.976	0.1	0.458	0.1	218
uPDW - PSW	0.863	0.1	0.535	0.1	219
AAW - PSW	0.598	0.1	0.449	0.1	
Sed. Pairwise Test					220
Fine Sed. - Pebbles	0.260	0.1	-	-	221
Fine Sed. – Fine w. pebbles	0.234	0.2	-	-	
Pebbles - Fine	0.819	0.1	-	-	222

Table 1 Results of Epifauna Two-Way Crossed ANOSIM (Analysis of Similarities) comparing epifauna community across all watermasses (unordered) and sediment groups (unordered) and One-Way ANOSIM comparing infauna community across all water masses (unordered). ANOSIM results utilised 999 permutations.

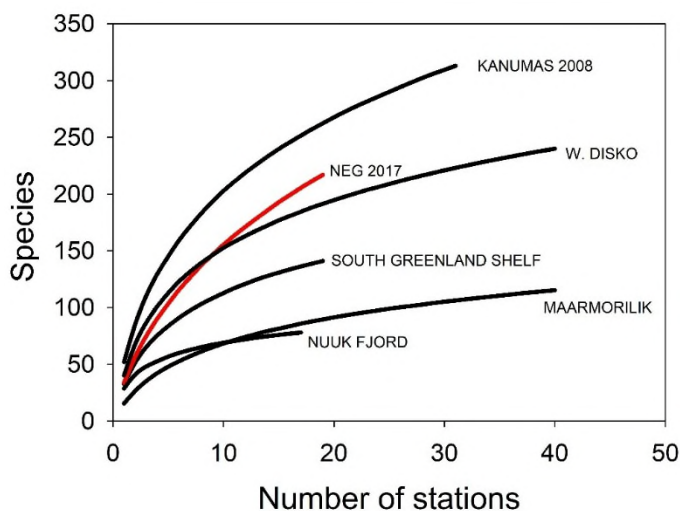


Fig. 4 Species accumulation curves for sampled stations from West Greenland shelves grouped by surveys and the corresponding species accumulation curves from NEG 2017 cruise (red line). Only arthropods and annelids are included. West Greenland habitats include fjords, banks, and shelf plains. The NEG 2017 cruise included fjords, shelf plains and shelf slopes.

NEG shelf study compared with previous studies on the WG shelves (including shelf plain, banks, fjords and shelf slopes) that have the sampling design, analytic methods and often the same taxonomic experts (Piepenburg et al. 2017). The NEG shelf was had 3-4 % of the biomass and 15% abundance found on the WG shelves (Fig. 5).

As annelids and arthropods are the most species-rich phyla on both shelves which could be identified down to species level, these were selected for direct comparison. On average, NEG shelf species richness of both phyla, was 2/3 of that WG shelves, whereas Shannon diversity was similar for both systems. The NEG shelf species represented 16 phyla, >298 species, within 73 0.1 m² samples and an average species richness of 18.5 and Shannon diversity 3.5 (Fig. 5).

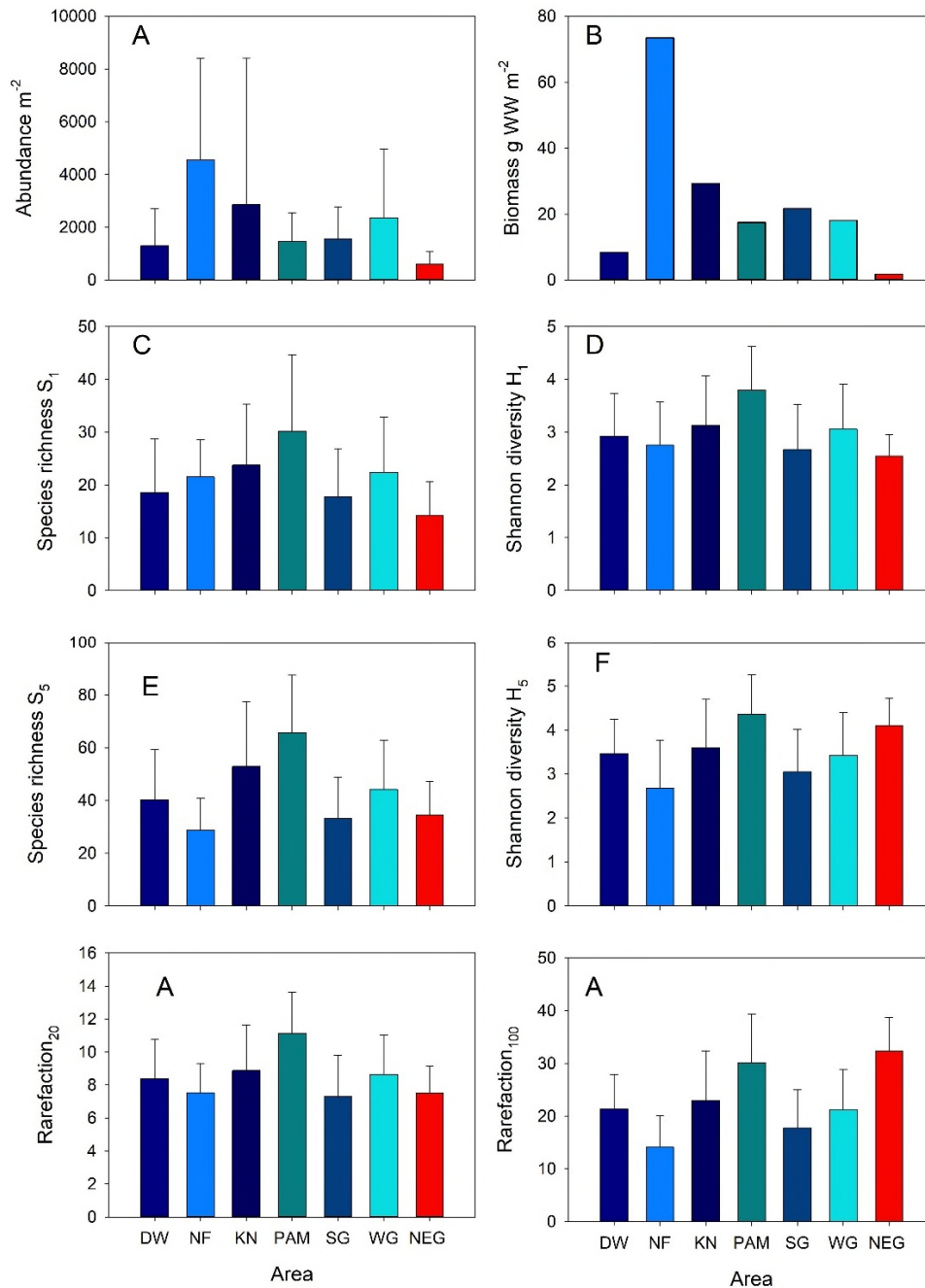


Fig. 5 Comparison of benthic communities from West Greenland benthos surveys on shelf plains, banks and fjords with corresponding data from Northeast Greenland (DW = Disko West 2009; NF = Nuuk Fjord 2008; KN= Kanumas 2008; PAM = South Greenland 2011; SG = South Greenland 2010; WG = all west Greenland investigations) and red column denotes present data from 2017 (NEG). All biodiversity measures were restricted to arthropods and annelids only. A) Total number of individuals per m². B) Total average biomass per m². C) Species richness S₁ = number of species per sample (0.1 m²). D) Shannon diversity H₁ per sample (0.1 m²). E)

Species richness S_5 = number of species per five sample (0.5 m²). F) Shannon diversity H_5 average for five accumulated samples. G) Rarefaction₂₀ the number of species of arthropods and annelids per 20 individuals. G) Rarefaction₁₀₀ the number of arthropod and annelid species per 100 individuals.

Discussion

The Arctic is currently undergoing system-wide changes driven by climate change (1-3), in particular changes to the upper 200m of the Arctic Ocean (5-8) are a result of warmer and saltier inflow of sub-Arctic Atlantic water, a phenomenon termed as ‘Atlantification’ and alter the behaviour of the NE polynyas (Michel et al. 2015). This ‘Atlantification’ also affect the NE Greenland ice shelf and will likely alteration food web, increased importance of boreal species, at the cost of arctic species and a greater sensitivity to further environmental change (Fredriksen et al. 2020). Addressing and predicting the future of NE Greenland shelf requires a knowledge of current conditions and how ongoing changes influence the benthic community.

Across the NE Greenland shelf a shift in community structure was found across all water masses, except RAW and AAW, a limitation of this study is depth and sediment type could not be completely isolated as factor as water masses may only be found at certain depth or the water mass comprised of a singular sediment type. It is noteworthy however that this pattern repeated in the epifauna and infauna communities with the RAW and AAW communities sharing a high abundance of Mysida, Ophiuroidea and Serpulidae taxa. RAW benthic communities also had low intra-group similarity, but the highest number of samples indicating that there is diversity within this group and potentially requires additional factors to fully understand. Previous work on the Arctic Barent Sea demonstrates a poleward shift in the distribution of warmer water species, such as commercial important fish and snow crabs (*Chionoecetes opilio*) with a reduced importance of Coldwater species (Ingvaldsen et al. 2021). If followed by trawling activity large sessile/vagile megafauna such as echinoids and pennatulids found on the NE Greenland shelf would be particularly vulnerable.

NE Greenland shelf had low abundance of annelids and arthropods compared to WG, however with low biomass, the large megafauna such as echinoid *Gorgonocephalus* sp. and pennatulids *Umbellula encrinurus*, was common on the video (a few individuals) so could represent a large component of the total community biomass. Station 49 was notably for its recent iceberg scour activity, with the high number of mobile macrofauna species (ophiuroids and crinoids) (Robinson et al. 2020) rapidly moving in after the scouring event to take advantage of the recently vacated niches and feeding opportunities (Vause et al. 2019).

Diversity assessment on alpha-diversity represents the diversity in the smallest spatial scale, beta-diversity represents diversity between sites or gradients, in this report we treat this as diversity amongst replicate sample and gamma-diversity as the diversity across the entire ecosystem. In contrast to low abundances, biomass and alpha-diversity, in the present NEG study, beta and gamma-diversity was similar or high than the WG studies (Fig. 4). Also evident in the species accumulation curves was the higher expected gamma-diversity of NEG overtaking all WG surveys if the total species pools were sampled. High gamma-diversity is typically associated with high habitat heterogeneity, however the WG studies covered a greater latitudinal range and sampled high productive banks, compared to this NEG survey. This suggest that diversity is higher on the NEG shelf than WG shelves when accounting for sampling effort and habitat characteristics.

All stations were almost completely covered by small stones and gravel, on top of a clay seabed, this strong sorting of sediment could indicate erosion of finer sediment at the surface (winnowing) leaving the larger stones at the surface. The surface stones could provide small-scale habitat heterogeneity within the benthic environment, increasing gamma-diversity, due to the stochastic placement and density of small surface stones and gravel. Any trawling activity would homogenise the seafloor, burrowing or removing small surface stones and gravel, removing the unique communities found on these stones. NEG shelf has currently has a low level of trawling leading to a relatively pristine environment, evidence for which can be seen in the *Umbellula encrinus* populations which would be particularly vulnerable to all kinds of disturbance and with populations estimated to be > 45 years old. Iceberg scour provides a similar source of natural disturbance events within this ecosystem but are rare within these depth and environment (Barnes and Conlan 2007).

The NEG shelf benthic community exhibited high gamma-diversity with low biomass and abundance and a high degree of benthic communities across the shelf overlaying on a what is a relatively homogenous shelf environment. The high gamma-diversity across the NEG shelf benthic community combined by the increase 'atlantification', subsequent trawling potential leaves its vulnerability to future disturbances, particularly small-scale acute disturbances such as trawling, which could completely remove any unique local heterogeneous benthic community with minimal fishing effort.

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