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# Influence of environmental parameters in modulating benthic and pelagic life cycle stages of macrobenthic population in high Arctic fjords: A modelling approach

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ABSTRACT

Macrobenthic recruitment is a critical process that underpins the structure and functioning of benthic ecosystems. This study delves into the different life cycle stages of macrobenthic communities from two high Arctic fjords, Kongsfjorden and Krossfjorden, Svalbard. Outer fjords and open ocean zones, characterized by higher total organic carbon (TOC) and fine-grained silty sediments, supported diverse assemblages dominated by polychaetes. Early settlers, including juvenile polychaetes, molluscs, and crustaceans, were especially abundant in these regions. Meroplankton communities were primarily composed of crustacean larvae, particularly Cirripedia. Hierarchical Modelling of Species Communities (HMSC) indicated that environmental variables, particularly sediment texture, TOC% and surface chlorophyll *a*, explained maximum variance proportion in taxon abundances. Sand% in sediment was positively correlated with adult molluscs and arthropods, while TOC% was crucial for early settlers and adult annelids, sipunculids. The model's high explanatory power ($R^2 = 0.883$) and robust fit demonstrate the significant influence of environmental factors in shaping Arctic fjord benthic communities. These results underscore the importance of ecological modelling in integrating macrobenthic life stages (larval, early settlers, and adult) which offers a cohesive framework to unravel settlement dynamics and the environmental processes shaping macrobenthic community structure in Arctic fjords.

## 1. Introduction

Macrobenthic organisms are essential components of benthic ecosystems which play a pivotal role in marine ecosystem functioning through their contributions to energy transfer, nutrient cycling, and benthic–pelagic coupling (Brey and Gerdes, 1998). Benthic-pelagic linking is a crucial juncture in the life of most macrobenthic organisms as they have a bipartite life cycle comprising both planktonic (mereplankton) and benthic phases (Morgan, 1995, Mandal et al., 2010). Environmental factors can influence meroplankton settlement rates thereby governing macrobenthic community structure (Menge, 2000; Shanks, 2009; Jennings and Hunt, 2010). However, the combined effects of these environmental gradients across multiple macrobenthic life stages are still not well understood.

The Arctic region especially fjords are highly influenced by ongoing global climate change (Walsh et al., 2011; Zhao et al., 2019). Arctic fjords are dynamic ecosystems with significant contributions to carbon cycling due to relatively high sedimentation rates (Faust and Knies, 2019) and strongly influenced by oceanic currents (Polyakov et al., 2005). Inflows of glacial meltwater from Arctic fjords, enriched with organic matter, significantly affect primary productivity and sediment characteristics. These processes in turn affect macrobenthic settlement patterns in the glacial bay (Gorlich et al., 1987; Syvitski, 1989). Furthermore, the glacial meltwater produces sharp gradients in abiotic factors along the fjord system (Hop et al., 2002; Kotwicki et al., 2004), that regulates the distribution of both benthic and pelagic entities (Piquet et al., 2014; Włodarska-Kowalczuk et al., 2016; Tripathy et al., 2023). Therefore, it is critical to study the connection between meroplankton and benthos along with environmental factors which shape the settlement processes from this eco-region.

In recent years, a few studies have focused either only on meroplankton or early settler dynamics from the Arctic fjords, but not

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encompassing all macrobenthic life cycle stages (Beuchel and Gulliksen, 2008; Yakovis et al., 2013). These stages represent critical junctures as they determine patterns of larval dispersal, settlement success, and subsequent macobenthic population structure (Morgan, 2001). Therefore, to gain a comprehensive understanding of the population dynamics of macrobenthos in Arctic fjords, it is essential to investigate both the pelagic phase and the early settlement period of their life cycle. Furthermore, early settlers which include macrofauna with direct development also falls under the meiobenthic size range establishing a stronger correlation between meiobenthic and macrobenthic communities.

Existing studies have predominantly employed multivariate ordinations to examine macrobenthic communities and their relationship with environmental parameters (Legendre and Legendre, 2012). However, these approaches often fail to optimally link the relationship between environmental gradiants and macrobenthic species interactions across different life stages (Thioulouse et al., 2018). This represents a critical knowledge gap because Arctic fjords experience pronounced environmental gradients that simultaneously drive environmental filtering and complex biotic interactions, however, traditional analyses fail to caputure these processes precisely (Zhulay et al., 2023). The present study addresses this fundamental limitation and is a pionner attempt to apply Hierarchical Modelling of Species Communities (HMSC) to understand the life cycle stages of macrobenthic communities inhabiting across Arctic fjords. HMSC has become an increasingly prominent tool in ecological research, offering a robust statistical framework to unravel the mechanisms driving biodiversity patterns (Zuur et al., 2022). Unlike conventional approaches that model species occurrences or abundances separately, HMSC allows for a joint modelling framework. This enables the partitioning of ecological variation into components attributable to environmental filtering, species-to-species associations, and stochastic processes within a unified framework (Bhaumik et al., 2025). The hierarchical framework of HMSC enables the assessment of variations in community composition as a function of changing environmental covariates (Ovaskainen and Abrego, 2020). This integrative approach allows researchers to derive mechanistic insights at both the species and community levels within a single coherent framework (Ovaskainen et al., 2017).

Against this backdrop, this study aims to: (1) document the variations of macrobenthic community structure, (2) investigate the role of environmental variables in structuring the macrobenthic settlement process and (3) link benthic and pelagic biotic components for understanding the contribution of meroplankton, and early settlers in shaping the adult macrobenthic community from Arctic fjords on a spatial scale from outer to inner fjords using hierarchical modelling approach. The present study is unique in several interconnected advancements that integrates macrobenthic life cycle stages (larval, early setters', and adults' abundance) within a unified analytic framework for assessing the population structure of macrobenthic species from the Arctic fjords. It also leverages HMSC's exceptional power to quantitatively partition the effects of environmental filtering versus biotic interactions. This combined approach provides a more mechanistic and comprehensive understanding of the processes that shape macrobenthic assemblages. It also overcome the limitations of previous descriptive studies and enhances predictions of ecosystem responses to environmental changes. Furthermore, this novel effort aims to improve our understanding of ecosystem processes regulating macrobenthic settlement dynamics occurring in these fjords.

## 2. Materials and methods

### 2.1. Study area

Kongsfjord, an open glacial fjord located in Ny-Ålesund on the western coast of Svalbard spans 20 km in length and 4–10 km in width (MacLachlan et al., 2010). Hydrographic conditions in the outer fjord are modulated by the dynamic interaction between intruding warm Atlantic and cold Arctic water masses (Cottier et al., 2005). Glacial inputs of freshwater and sediments create a gradient in environmental parameters progressing towards the inner fjord (Hop et al., 2002). Adjacent to Kongsfjord lies Krossfjord, forming a connected fjordic system known as the Kongsfjord–Krossfjord system (78°50′–79°30′N and 11°–13°E), which converges into a deep glacial basin the Kongsfjordrenna (Saraswat et al., 2018). Kongsfjord, the southern arm of the system, is oriented in a southeast-northwest direction, while Krossfjord, the northern arm, is aligned in a north-south direction (Svendsen et al., 2002).

### 2.2. Sample collection

#### 2.2.1. Environmental parameters

Surface and bottom water samples were obtained from each station with a Niskin water sampler for the analysis of chlorophyll *a* (Chl *a*) and phaeopigments. 1 L sample of seawater was collected in an amber bottle and subsequently filtered through a glass fiber filter (GF/F, 0.7 μm pore size). In the laboratory, pigments were extracted from the filter paper using 90 % acetone and stored overnight at 4°C, with concentrations determined spectrophotometrically (Nandy et al., 2018). A 100 mL aliquot of water was transferred into pre-cleaned polypropylene tubes and stored frozen at −20°C for nutrient analysis. Nitrate ($NO_3$), nitrite ($NO_2$), phosphate ($PO_4$), ammonium ($NH_4$), and silicate ($SiO_4$) concentrations were quantified using a continuous segmented flow autoanalyzer (Model-AA3, Seal Analytical Ltd., Germany) following JGOFS protocols (Intergovernmental Oceanographic Commission, 1994), with a standard error of less than 2 % for all triplicate analyses.

Sediment samples were collected to examine the influence of environmental parameters on the structure of biotic communities.Total organic carbon (TOC) concentration was estimated by wet oxidation method using $H_2CrO_4$ digestion and further titrated against 0.2 N Fe $(NH_4)_2(SO_4)_2{\cdot}6H_2O$ solution (El Wakeel and Riley, 1957). Sediment granulometry was quantified using pipette analysis (Buchanan, 1984). Chl *a* concentration in sediment was measured via the 90 % acetone extraction method (Strickland and Parsons, 1972).

#### 2.2.2. Biological component

Sediment samples were collected from 13 stations (6 from Kongsfjorden, 5 from Krossfjorden, and 2 in Open Ocean) (Fig. 1) during June-July 2023 using Van Veen grab. Macrobenthic samples were sieved in situ through a 0.5 mm sieve and preserved in 4 % rose bengal buffered formalin for further taxonomic analysis. After transport to the laboratory, macrobenthic specimens were sorted and identified to the lowest possible taxonomic level using a stereo zoom and compound microscope with an attached camera, following standard taxonomic references (Southern, 1921; Fauvel, 1953; Day, 1967; Gagaev, 2009; Bodil et al., 2011; Dnestrovskaya and Jirkov, 2012). Photographic cataloging has been made of the identified specimens. Obtained numerical data were converted to individuals per $m^2$ (indv. $m^{-2}$).

For early settlers, from each grab replicate samples were taken using hand-held acrylic corer (inner diameter 5 cm) and preserved in the same manner as macrobenthos. Samples were washed through 500 μm and 63 μm sieves to separate adults from early settlers (Pfannkuche and Thiel, 1988). Sediments retained on the 63 μm mesh were processed using the floatation technique (Armenteros et al., 2011). Early settlers were identified to higher taxonomic levels and counted under a stereo-zoom microscope, with density expressed in indv. 10 $cm^{-2}$. Following enumeration, early settlers were sorted and mounted on glass slides using the formalin–ethanol–glycerol method (Seinhorst, 1959). Identification was performed using a compound microscope with a camera, referencing standard literature (Shanks, 2001; Strathmann, 2017).

Meroplankton samples were collected from each station using a plankton net with a 100 μm mesh size and a 0.6 m ring diameter,

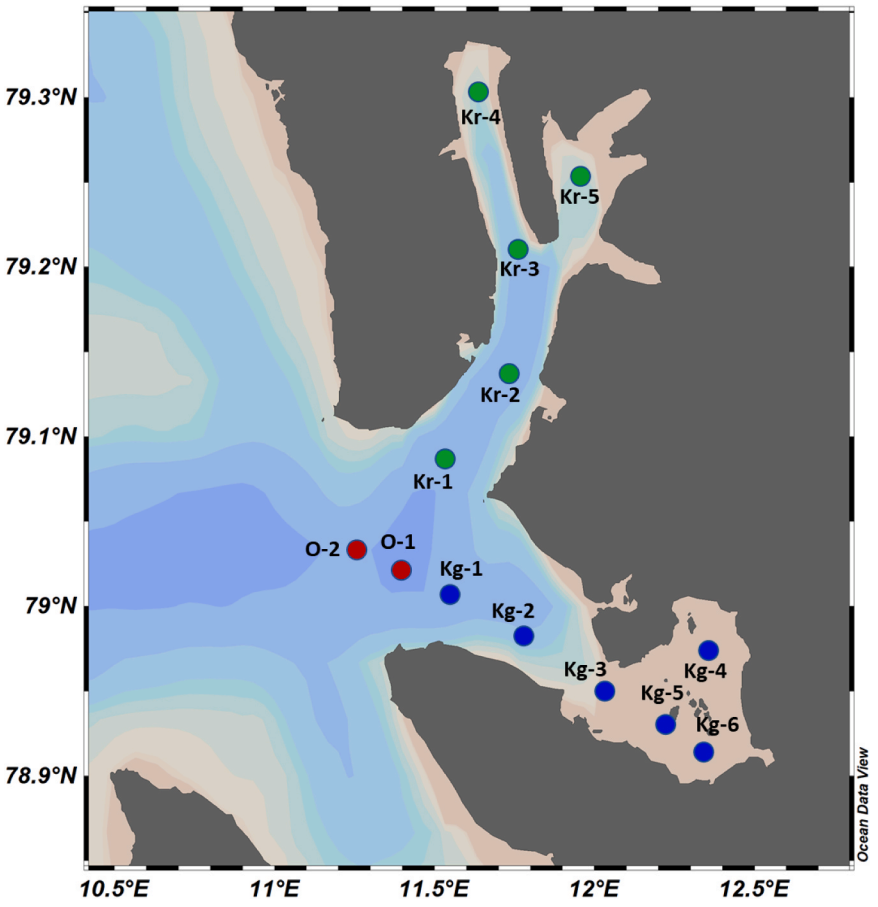



**Fig. 1.** Map showing the sampling locations in the high Arctic fjords (Open Ocean: O, Kongsfjorden: Kg, and Krossfjorden: Kr). Numeric digits denote station numbers in these fjords.

equipped with a digital flow meter (Hydro Bios). All collected samples were preserved in 4 % buffered formalin and further identified under binocular stereo-zoom and compound microscope. Numerical abundance was expressed as indv. $m^{-3}$ . Taxonomic identification of the meroplankton samples was conducted following established protocols (Conway et al., 2003; Al-Yamani et al., 2011; Ardyna and Arrigo, 2020).

### 2.3. Data analysis

A boxplot of scaled values was generated to standardize units and visualize the range and distribution of environmental variables, Species–environment relationships were analysed using Hierarchical Modelling of Species Communities (HMSC), a Bayesian joint species distribution framework implemented via the 'Hmsc' R package v.3.0–13 (Ovaskainen et al., 2017; Tikhonov et al., 2020). The model assessed the responses of adult, early settlers, and meroplanktonic macrobenthic taxa to environmental gradients using a Gaussian distribution with a normal link function. Posterior distributions were sampled through five Markov Chain Monte Carlo (MCMC) chains and the details of the model parameters have been provided in Supplementary Data S1. Convergence was evaluated using potential scale reduction factors (Gelman and Rubin, 1992). Variance partitioning was conducted to quantify the relative contributions of fixed effects (environmental variables) and random effects (station), following the approach outlined in Ovaskainen et al. (2017).

## 3. Results

### 3.1. Environmental parameters

The box plot illustrated spatial environmental variability in hydrographic and sediment parameters from high Arctic fjords (Fig. 2). All the surface water parameters except $PO_4$ showed a wide interquartile range (IQR), with $NH_4$, $NO_2$, Chl *a*, and phaeopigments being positively skewed (Fig. 2a). In contrast, bottom water parameters exhibited relatively stable distributions, with nitrate showing the greatest variations (Fig. 2b). Sediment-related variables such as depth, Chl *a*, and phaeopigments displayed wide IQRs (Fig. 2c). Parameters like TOC% and sand % showed least spatial variations during the study period. TOC% exhibited a positively skewed distribution with a few outliers, while depth and clay% displayed negatively skewed distributions (Fig. 2c). Interestingly, our results also portrayed that TOC concentrations were significantly higher in the open ocean and outer fjord regions, suggesting enhanced organic matter deposition in these areas. Across all sampling stations, silt is the dominant sediment type, followed by clay%, indicative of a fine-grained depositional environment. For comprehensive reference, spatial variations of surface and bottom water quality parameters across the thirteen study stations are provided in Supplementary Fig. 1. Furthermore, corresponding variations in environmental factors and sediment texture composition are illustrated in Supplementary Fig. 2.

### 3.2. Taxonomic composition and distribution pattern

Adult macrobenthic composition of Arctic fjords consists of 6 major phyla, Annelida, Arthropoda, Echinodermata, Mollusca, and Sipuncula.

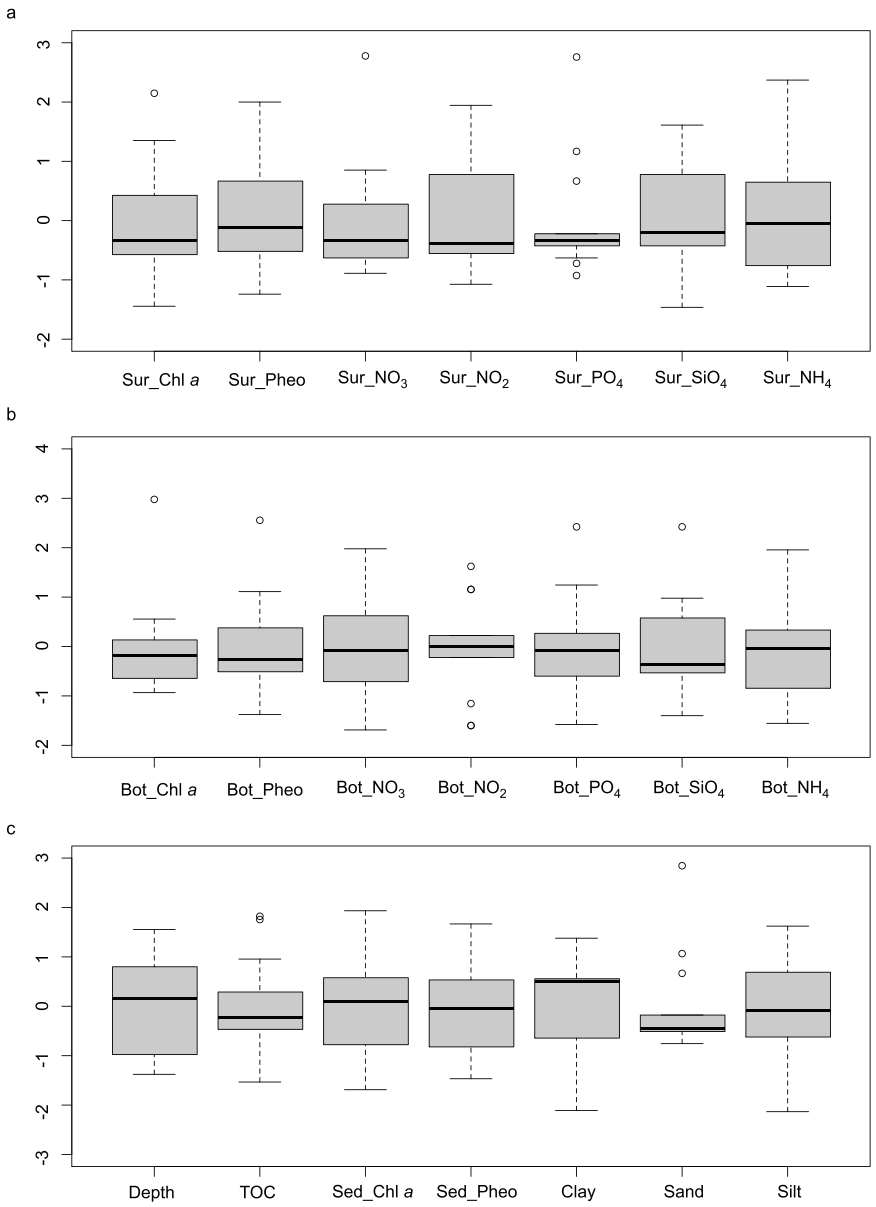



**Fig. 2.** Scaled boxplot showing spatial variation of environmental parameters from the study stations in high Arctic fjords: a. Surface water; b. Bottom water; c. Sediment.

Annelids were the most dominant among all the phyla constituting more than 50 % of the total abundance recorded from both the Arctic fjords (Fig. 3a). The macrobenthic communities of arctic fjords were dominated by the families Maldanidae and Yoldiidae with abundances ranging from 3867 to 9715 indv. $m^{-2}$. Early settlers were represented by juvenile polychaetes, oligochaetes, sipunculids, decapods, cumaceans, tanaidacea bivalves, and gastropods (Fig. 3b). Notably, polychaete juveniles were especially prevalent within this early settler group, with dominant families including Lumbrineridae, Spionidae, Maldanidae, Nephtyidae, and Glyceridae. Settler abundance was consistently higher in the open ocean and outer fjords than in inner fjords, with Kongsfjorden showing higher abundance than Krossfjorden. The meroplankton community was dominated by crustacean larvae, followed by molluscs (Fig. 4). The crustacean larva mostly constituted of Cirripedia. Mysis, Zoea, Megalopa, Nauplii were some other less-represented crustacean larvae recorded from the fjords. Macrobenthic abundance was found to be highest in the open ocean and outer fjord areas and comparatively lower in the inner fjords.

### 3.3. Hierarchical modelling of species communities (HMSC)

#### 3.3.1. Model convergence and fit

The model exhibited strong convergence, with potential scale reduction factors close to 1 for all parameters, indicating stable and well-mixed Markov Chain Monte Carlo (MCMC) chains (Supplementary Data S1). Effective sample sizes (mean: 11,488.63; median: 8982.20) demonstrated high sampling efficiency and statistical independence, supporting robust posterior inference. The mean explanatory power of the model ($R^2 = 0.883$) indicates that approximately 88.3 % of the variation in taxon abundance was captured. Model fit was exceptionally high ($R^2 > 0.95$) for adult molluscs, all early settler taxa (Annelida, Arthropoda, Mollusca, Sipuncula), and arthropod larvae, underscoring the model's reliability in representing the structure of Arctic fjord macrobenthic communities.

#### 3.3.2. Variance partitioning and species-environment relationship

The fixed effects explained 98.2 % of the total variance for macrobenthic adult, early settlers, and larval taxa recorded for the Arctic fjords

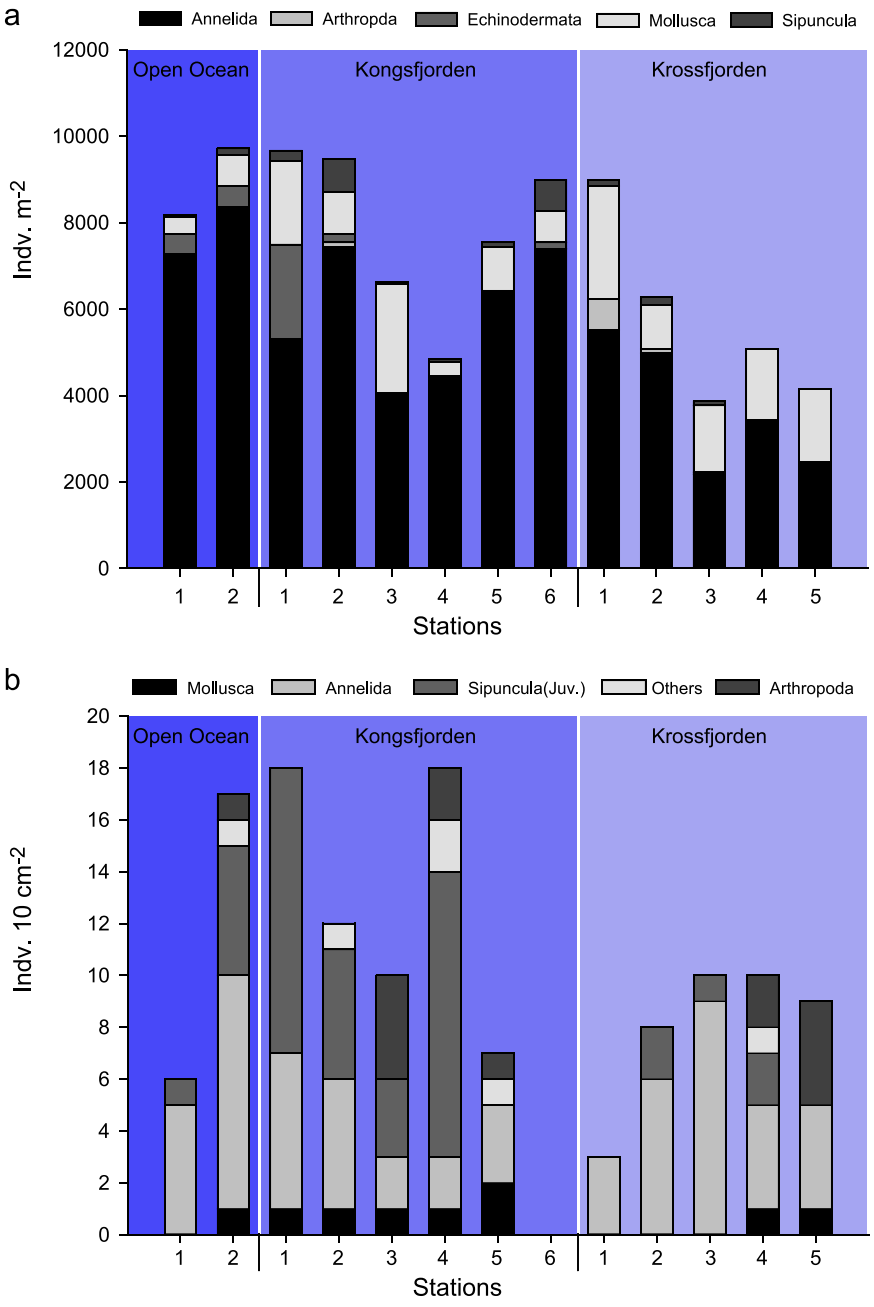



**Fig. 3.** a. Abundance of different groups of macrobenthos (indv. $m^{-2}$) across the studied stations, b. Abundance of different taxa of early settlers (indv. 10 $cm^{-2}$) across the studied stations.

(Fig. 5). Among the fixed effects, surface nutrients collectively explained 23.6 % of the variability with $NO_3$ explaining 7.2 % of the variance (Fig. 5). Bottom nutrients followed next collectively explaining 17.1 % variance with $NO_2$ contributing most of it. Sediment texture and TOC accounted for an average of 16 % and 11.7 % variance respectively for all taxa. Sand% in the sediment explained 8.6 % variance for all taxa recorded from the study area. Among other environmental parameters surface Chl *a* explained 9.5 % variability, followed by surface $PO_4$ (6.1 %). Station as the only random effect, explained an average 1.8 % variance of different life history stages of macrobenthic taxa occurrence (Fig. 5). TOC% in sediment explained more than 20 % variance of adult annelids and sipunculids. Furthermore, TOC% explained 16.2 % variance of early settler annelid taxa recorded from the fjords. Chl *a* in surface water interestingly explained almost 16 % of the total variance for arthropod meroplankton community. The fixed effect of sediment sand% was most noticeable in adult arthropoda and mollusca which explained about 15 % and 19 % of the total variance, respectively (Fig. 5). Adult macrobenthic taxa recorded from the study area showed a positive correlation with sediment Chl *a* and phaeopigment at 0.50 support level. Early settlers of phylum annelida showed high positive correlation with TOC% (Fig. 6). Several macrobenthic life cycle stages exhibited distinct correlations with TOC%, sand%, surface water $NH_4$, and bottom water $PO_4$. Detailed associations and support values are presented in Table 1.

## 4. Discussion

Macrobenthic invertebrates exhibit diverse larval dispersal strategies to ensure successful settlement, often characterized by distinct feeding modes such as planktotrophy or lecithotrophy. Extended pelagic larval

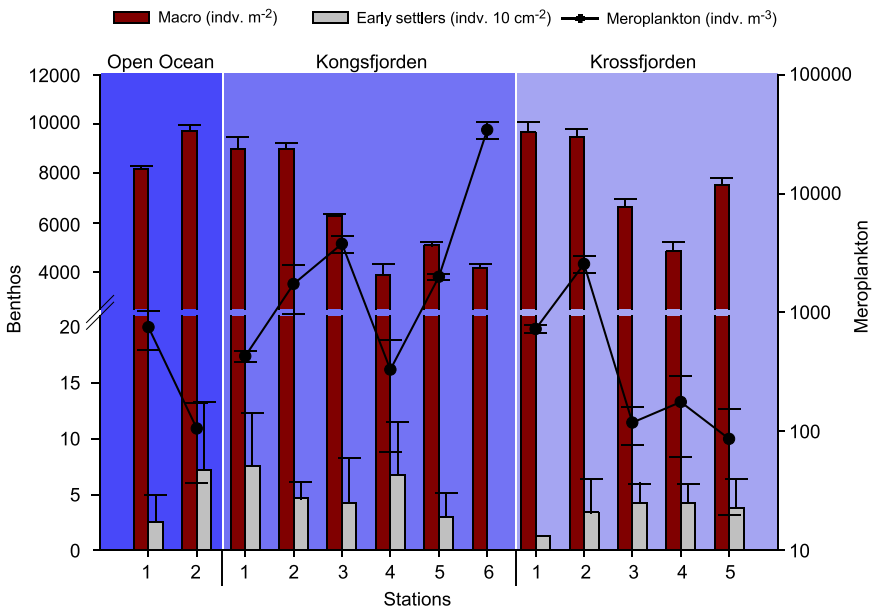



**Fig. 4.** Spatial variation in the different components of benthic and pelagic community in high Arctic fjords. The bar plot and line plot show the abundance of benthos and meroplankton respectively.

duration increases dispersal and colonization potential thereby influencing adult distribution patterns (Fetzer and Arntz, 2008). By studying only the benthic phase of the life cycle, it is virtually impossible to draw a conclusion about the population dynamics. This study highlights the importance of benthic-pelagic linking in Arctic fjords, Kongsfjorden and Krossfjorden, where complex interactions between these zones are pivotal in shaping macrobenthic community. In Arctic fjords, fluctuations in organic matter flux strongly affect benthic organisms, with higher TOC levels in outer fjord and open-ocean areas linked to greater macrobenthic abundance (Włodarska-Kowalczuk et al., 2019). Higher macrobenthic and settlers abundance in outer fjords and open ocean areas results from enhanced organic carbon availability (Zaborska et al., 2018). These zones consistently exhibit elevated TOC concentrations from convergence of marine-derived organic matter (Hop et al., 2002; Włodarska-Kowalczuk et al., 2019), creating favorable conditions for larval settlement. According to HMSC results annelid settlers positively correlated with TOC%, that indicates organic-rich sediments promote their settlement and growth. Fetzer et al. (2002) reported an almost perfect correlation between juvenile polychaete abundance and TOC in Kongsfjorden sediments. Włodarska-Kowalczuk and Pearson (2004) similarly found that polychaete densities in Hornsund fjord covaried positively with sediment TOC concentration. Renaud et al. (2008) further demonstrated an increase in the abundance of deposit-feeding polychaetes from Arctic shelves in response to elevated organic carbon inputs. Silt and clay sediments in combination with high TOC supports diverse and abundant macrobenthic communities dominated by families like Maldanidae and Yoldiidae (Zaborska et al., 2018). The outer fjords benefit from stable Atlantic Water intrusion that enhances nutrient availability and primary productivity without the detrimental effects of excessive glacial sedimentation (Hop et al., 2002; Cottier et al., 2005), while fine-grained silty sediments provide optimal substratum for successful settlement. Interestingly, our results have shown that areas with higher sand content, often found near the outer parts of the fjords, support higher species richness and biomass of macrobenthic fauna due to better oxygenation and substrate stability (Włodarska-Kowalczuk, 2007). Both variance partitioning and species-environment relationships depicted that sandy substratum favoured macrobenthos belonging to phylum mollusca and arthropoda in arctic fjords. Sandy substrates offer higher permeability and oxygen availability, creating favorable conditions for burrowing and suspension-feeding bivalves and amphipods (Gusev and Rudinskaya, 2014; Tamaki et al., 2018). According to Krishnapriya et al. (2019) water depth significantly shape macrobenthic community structure in these fjords through its influence on sediment texture and organic input.

In our study area, meroplankton community was dominated by crustacean larvae, followed by molluscs, that reflects a typical Arctic fjord composition (Kuklinski et al., 2013; Stübner et al., 2016). Among crustaceans, cirripeds were predominant, while other forms such as mysis, zoea, megalopa, and nauplii were less represented. The dominance of cirripeds and bivalve larvae during early summer coincides with the phytoplankton bloom which underscores the excellent synchronization of high pelagic productivity and reproductive output (Kuklinski et al., 2013; Stübner et al., 2016). Cirripedia nauplii were only found from late April to early July (Stübner et al., 2016). Their findings revealed two distinct peaks in abundance during the peak Chl *a* period, with one occurring in early May and other at the end of May (Stübner et al., 2016). In June–July, Cirripedia were mainly represented as cyprids of *Balanus balanus*, corresponding to very low Chl *a* biomass in July. The species produces a single brood annually, with nauplii released after about 40 days of embryonic development (Barnes and Barnes, 1954), and larval densities reaching up to 30,000 indv. $m^{-3}$ during spring bloom conditions in Svalbard fjords. Adult of *B. balanus* are similarly abundant in Kongsfjorden, with average densities of 489.7 indv. $m^{-2}$ at depths of 10–30 m (Voronkov et al., 2013; Wiencke and Hop, 2016). Although adult and early settlers were most abundant in outer fjords, larval densities peaked at mid-fjord stations, likely due to hydrodynamic retention by eddies and gyres (Stübner et al., 2016). Stratification from glacial meltwater inputs forms density gradients that promote larval retention in mid-fjord basins (Michelsen et al., 2017). According to Myksvoll et al. (2014) a persistent eddy in Sørfolda trapped cod eggs in the central fjord which substantially prolonged their residence period compared to areas outside the eddy. Such processes explain the observed accumulation of meroplankton in the middle and inner fjords (Wiencke and Hop, 2016). These patterns reflect that organic carbon flux and seasonal productivity regulates larval settlement success.

The observed positive correlations between most macrobenthic adults, early settlers, and meroplankton taxa with sediment Chl *a* and phaeopigments highlight the pivotal role of phytodetritus deposition in structuring benthic and pelagic communities in Arctic fjord systems.

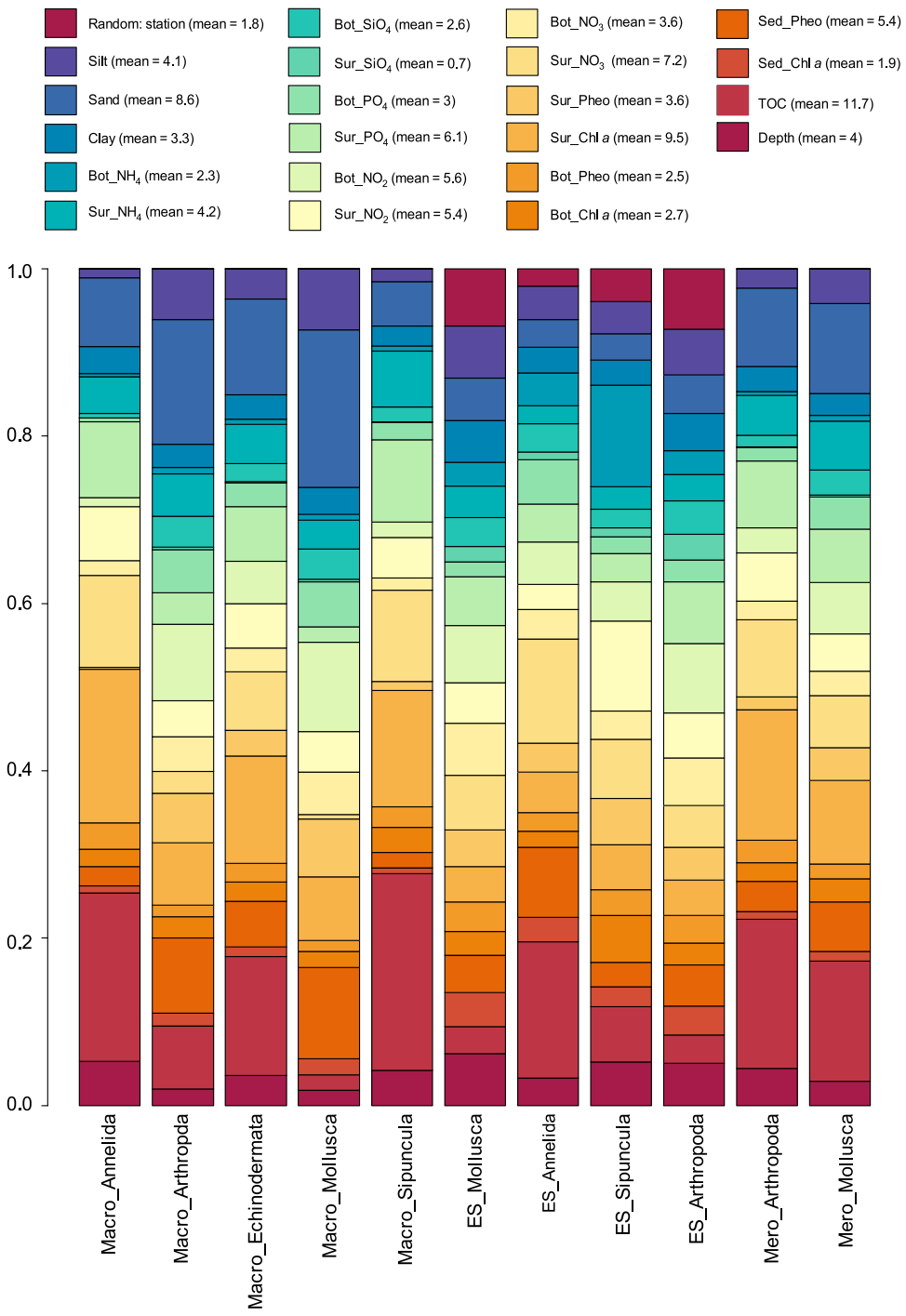



**Fig. 5.** Variance partitioning of environmental variables explaining proportion of macrobenthic life cycle stages; larvae, early settlers, and adult taxa from high Arctic fjords.

This is consistent with previous findings that sea-ice decline, has enhanced phytoplankton bloom increasing benthic algal production in Arctic fjords (Morata et al., 2020). The resulting higher input of algal material likely supports greater settlement and survival of benthic organisms, reflecting ecosystem responses to ongoing environmental shifts. The positive correlation of adult molluscan abundance with sediment Chl *a* underscores phytodetrital inputs as a key food driver in Arctic benthic systems. Roy et al. (2014) found that megabenthic biomass and density across the Canadian Arctic shelf increased with sediment Chl *a*, indicating richer communities where phytodetritus deposition is higher. McMahon et al. (2006) demonstrated that ice-algal and phytoplankton additions in Ny-Ålesund elevated sediment Chl *a* and fueled rapid consumption by deposit-feeding molluscs. Similarly, Carroll and Ambrose (2012) reported that macroinfaunal and specifically molluscan biomass on the northern Svalbard shelf co-varied positively with sediment pigment concentrations. Bivalves reproduce following the phytoplankton bloom which explains the moderate abundance of bivalve veliger during the study period. Contrastingly, negative correlations of adult molluscan taxa with bottom water $PO_4$ and sediment TOC% indicate sensitivity to nutrient enrichment and organic accumulation (Grebmeier et al., 2006). The positive correlation between arthropod meroplankton and surface water $NH_4$ likely results from

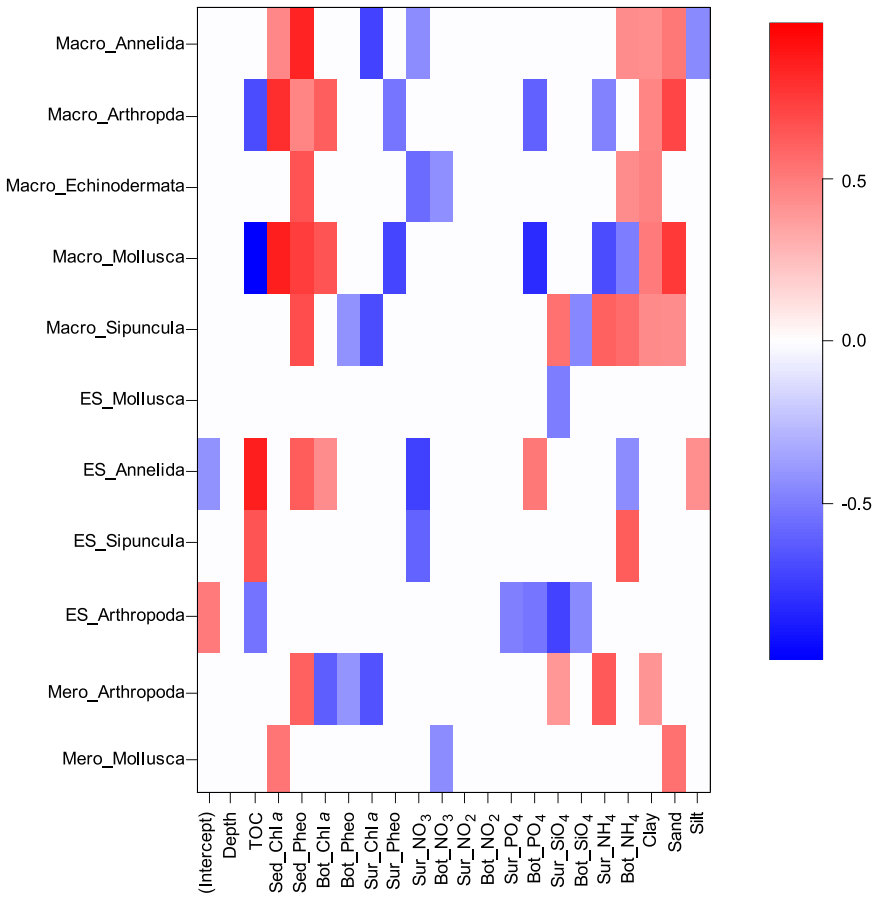



**Fig. 6.** The posterior support values for species-environment relationships across life cycle stages of macrobenthic taxa from high Arctic fjords (support level = 0.70). Positive correlations between species and environmental variables are indicated in red, while negative correlations are shown in blue. Relationships with weak statistical support are displayed in white.

**Table 1**
Summary of major taxa–environment relationships derived from HMSC correlations.

| Environmental Variable | Major Associated Taxa / Life Stage | Type of Correlation | Statistical Support Level | Ecological Interpretation |
|---|---|---|---|---|
| Sediment Chl *a* & Phaeopigments | All adult taxa | Positive | 0.5 | Indicates phytodetritus-driven food availability promote adult macrobenthic community |
| TOC% | Early Settlers (Annelida) | Strong Positive | 0.9 | Organic-rich sediments enhance annelid settlement success |
| TOC% | Adult Mollusca | Negative | 0.8 | Excess organic loading reduces oxygen, limiting molluscan population |
| Sand% | Adult Mollusca and Arthropoda | Positive | 0.8 | Sandy substrates provide oxygenated, stable conditions that support burrowing and suspension-feeding taxa |
| Surface Water $NH_4$ | Meroplankton (Arthropoda) | Positive | 0.8 | Reflects nitrogen demand and metabolic activity during crustacean larval development |
| Bottom Water $PO_4$ | Adult Mollusca | Negative | 0.8 | Phosphate enrichment linked to organic accumulation that reduces habitat suitability for sensitive taxa |
| Sediment Chl *a* | Adult Mollusca | Positive | 0.8 | Demonstrates dependence of adult molluscs on phytodetrital inputs for feeding |

ammonia excretion, a key process for maintaining nitrogen balance during early larval stages (Weihrauch and Allen, 2018; White, 2018). The absence of Echinoderm and Gastropod larvae during the sampling period is likely due to their delayed breeding relative to the blooming period (Kuklinski et al., 2013). Notably, the early settlers in Kongsfjorden outnumbered those in Krossfjorden, possibly due to Kongsfjorden's greater exposure to open oceanic waters, which enhances pelagic nutrient input (Wiencke and Hop, 2016). The present study provides a comprehensive understanding of the population dynamics of macrobenthos in Arctic fjords by integrating all life cycle stages, including larvae, early settlers, and adults. Although this study is based on a single sampling event undertaken during the summer of 2023, it captures a critical period of peak biological activity essential for understanding macrobenthic settlement dynamics across high Arctic fjords. Peak phytoplankton productivity following polar night enhances food availability, promoting larval survival and settlement (Berge et al., 2020). Benthic invertebrates exhibit reproductive synchrony with this bloom, making post-bloom months the optimal window for studying meroplanktonic and early benthic stages (Michelsen et al., 2017; Renaud et al., 2020).

In the context of future climate change, studies have confirmed that the Arctic is warming at a rate nearly three times faster than the global average (Parkinson and Comiso, 2013; IPCC, 2021). This rapid warming has resulted in widespread sea ice loss, glacier retreat, and increased ocean temperatures. These changes are causing significant shifts in oceanographic processes, circulation patterns, and water column biogeochemistry in Arctic fjords, which are especially modulated by environmental perturbations (Stroeve et al., 2007; Wassmann et al., 2011; Hopwood et al., 2018). Climate-driven transformations continue to reshape the physical and ecological dynamics of fjord systems and have cascading effect on macrobenthic communities residing in fjords (Włodarska-Kowalczuk et al., 2012). These communities are particularly sensitive to variations in glacial sediment input, episodic hypoxic conditions, and the increasing influence of warmer Atlantic waters (Włodarska-Kowalczuk et al., 2012; Zaborska et al., 2018). Climate change–driven modifications in organic carbon fluxes, water column stratification, and glacial meltwater inputs may substantially influence macrobenthic larval settlement success. Anticipated upsurge in primary productivity and shifts in organic matter export affect the quality and quantity of food availability to macrobenthic juveniles, that potentially may alter early post-settlement survival and growth (Lannuzel et al., 2020). Enhanced stratification related to sea-ice decline and increased freshwater discharge reduces vertical nutrient transport, that may weaken coupling of benthic- pelagic life cycle stages and alter their seasonal timing of food availability (Tremblay et al., 2015; Ardyna and Arrigo, 2020). Increased inputs of glacial meltwater may also alter sedimentation dynamics which in-turn will affect the benthic food quality, and consequently impair settlement success and community composition (Meire et al., 2017; Hopwood et al., 2018). Additionally, shifts in sediment characteristics driven by increased glacial discharge and coastal erosion may enhance fine-grained sediment deposition and organic matter burial, thereby affecting TOC availability and sediment composition (Macdonald et al., 2015). The HMSC model used in this study provides a valuable framework for forecasting how Arctic fjord ecosystems may respond to future environmental changes. The present study also provides valuable preliminary insights into environmental drivers that encompasses both planktonic and benthic phases of macrobenthic life cycle, while underscoring the need for future long-term, multi-seasonal studies to fully elucidate these complex processes across temporal scales. By integrating species diversity and environmental gradients, our study emphasizes the need for robust predictive models to forecast macrobenthic responses to environmental changes in Arctic fjords amid ongoing climate change scenario.

## 5. Conclusion

This study highlights the importance of benthic-pelagic linking and focuses on the role of environmental variables in structuring the macrobenthic population of Arctic fjords. Spatially, outer fjords and open ocean zones hosted higher adult and settler abundances, while mid-fjord areas supported elevated larval densities, likely due to hydrodynamic retention. Hierarchical Modelling of Species Communities (HMSC) revealed that TOC%, surface Chl *a* were major predictors in positively influencing annelid juveniles and meroplankton. Meroplankton abundance in the water column was found to be synchronized with the phytoplankton bloom. As May-June is considered the peak blooming period in this area, we recorded the highest abundance of meroplankton during the June-July phase with a greater abundance of crustacean larvae. Interestingly, the dominance of Cirripedia in the meroplankton community and its positive association with surface $NH_4$ may be attributed to their excretion process which maintains nitrogen homeostasis during early developmental stages. Adult molluscs showed negative correlations with TOC% and bottom $PO_4$ concentration, indicating potential sensitivity to organic enrichment. Sandy sediments supported higher abundances of molluscs and arthropods, reflecting preferences for stable, oxygen-rich habitats. The observed differences between Kongsfjorden and Krossfjorden in larval distribution and abundance emphasize the influence of environmental parameters and benthic-pelagic interactions on ecosystem productivity. These patterns highlight the role of benthic-pelagic linking and environmental filtering in structuring Arctic macrobenthos. Our findings emphasize the need to consider full life-cycle stages and seasonal variability for accurate predictions of community responses under accelerating climate change in Arctic fjords.

## CRediT authorship contribution statement

**Snigdha Bhaumik:** Writing – original draft, Formal analysis, Data curation. **Soumya Subhra Baishnab:** Writing – review & editing, Formal analysis, Data curation. **Ahmed Shahir:** Writing – review & editing, Formal analysis, Data curation. **Sumit Mandal:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Sarat C. Tripathy:** Writing – review & editing, Formal analysis, Data curation.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.rsma.2025.104615.

## Data availability

Data will be made available on request.

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# From conservatism to lability: Phylogenetic signal and evolutionary models decode macrobenthos functional trait evolution from high Arctic fjords

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Evolutionary model

ABSTRACT

The macrobenthic communities play crucial ecological roles in Arctic fjords. This study integrates mitochondrial cytochrome *c* oxidase subunit I (mtCOI)-based phylogenies with functional trait data for 50 species from Kongsfjorden–Krossfjorden, Svalbard to investigate evolutionary constraints shaping trait variation. Phylogenetic signal (PS) was quantified across 21 traits using Pagel's $\lambda$, Blomberg's K, Moran's I, and Abouheif's $C_{mean}$. Most traits exhibited strong PS (Pagel's $\lambda \geq 1.0$, $p = 0.001$), indicating pronounced evolutionary conservatism among Arctic macrobenthos. Tube-dwelling ($C_{mean} = 0.310$, $p = 0.002$) and burrowing (Moran's I = 0.053, $p = 0.004$) traits exhibited the highest autocorrelation, which reflects adaptation to extreme Arctic fjord conditions. Feeding and environmental position traits showed strong PS and autocorrelation, while reproductive traits were evolutionarily labile. Phylogenetic correlograms revealed hierarchical evolutionary constraints with strong conservatism in living habitat, intermediate constraint in feeding habits, and high lability in reproductive strategies across Arctic macrobenthic assemblages. Phylogenetic principal component analysis highlighted major axes of trait variation structured by shared ancestry. Evolutionary model fitting identified Early Burst (EB) as the best model for overall trait evolution, suggesting rapid initial diversification followed by evolutionary deceleration. Univariate traits showed mixed patterns, with environmental position following EB, while body size and motility evolving gradually under Brownian Motion model. These findings provide novel insights into complex evolutionary dynamics where deep phylogenetic constraints coexist with functional flexibility.

## 1. Introduction

The Arctic is undergoing rapid warming, nearly three times faster than the global average (Parkinson and Comiso, 2013; IPCC, 2021). This warming has led to widespread reductions in sea ice cover, retreat of glacier fronts, and an increase in ocean temperatures (Wassmann et al., 2011). Arctic fjords are particularly sensitive to these changes in oceanographic conditions, circulation patterns, and water column biogeochemistry (Stroeve et al., 2007; Hopwood et al., 2018). Kongsfjorden and Krossfjorden on the western coast of Spitsbergen exemplify these transformations, showing clear signs of glacial retreat, reduced sea ice, and increasing Atlantic water intrusion—a process termed "Atlantification" (Svendsen et al., 2002; Berge et al., 2016). Despite these changes, the inner fjord remains influenced by glacial runoff (Sundfjord et al., 2017; Torsvik et al., 2019) and continues to support a dynamic mix of Arctic and boreal species (Voronkov et al., 2013; Molis et al., 2019; Kokarev et al., 2021; Molina, 2023).

Fjords are characterized by large spatial contrasts in sedimentation, oxygenation, and habitat stability. While Arctic warming continues to reshape the physical and ecological dynamics of fjord systems, these shifts have significant implications for macrobenthos (Włodarska-Kowalczuk et al., 2012). The macrobenthic communities residing in these fjords are extremely sensitive to changes in glacial sediment input, hypoxia events, and the increasing influence of warmer Atlantic waters (Włodarska-Kowalczuk et al., 2012; Zaborska et al., 2018). Macrobenthos in fjord systems mediate essential ecosystem processes like bioturbation and bio-irrigation, facilitate organic-matter remineralisation and nutrient cycling, and act as a crucial trophic bridge between benthic and pelagic realms (Kristensen et al., 2012; Freitas et al., 2022). As these organisms influence organic-matter burial and supply of resources to higher consumers, shifts in macrobenthic diversity or trait composition can cascade through food webs and can alter crucial ecosystem functioning (Snelgrove, 1997; Thrush et al., 2006; Gladstone-Gallagher et al., 2017).

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Functional trait approaches have provided a powerful means to link biodiversity changes with ecosystem functioning (Kokarev et al., 2017; Liu et al., 2019; Käß et al., 2021). Traits and their modalities, like body size, habitat position, feeding mode and reproductive strategy, explain ecosystem processes more directly than only taxonomic studies (Beauchard et al., 2017). Integrating taxonomic and functional perspectives improves our understanding of benthic community structure and better informs conservation and management (Hajializadeh et al., 2020; Delfan et al., 2021; de Souza et al., 2021; Miri et al., 2023). However, species or higher taxa are not statistically independent: they are arranged in nested phylogenies, and their shared ancestry can shape trait distributions (Sakamoto and Venditti, 2018). Two broad evolutionary processes act on trait evolution in opposing ways. Adaptive radiation promotes rapid diversification of lineages and their traits under novel ecological opportunities or biotic interactions, whereas niche conservatism reflects the retention of ancestral ecological characteristics (Ackerly, 2003, 2009). Disentangling whether trait distributions in macrobenthos reflect recent adaptive responses to present-day environments or deep phylogenetic constraints is key to understand how communities assemble and persist under constant environmental change, an area of science perplexing evolutionary biologists (Losos, 2008; Cooper et al., 2010; Swenson, 2013).

Phylogenetic comparative methods (PCMs) explicitly account for phylogenetic non-independence and quantify Phylogenetic Signal (PS). In general, PS describes the tendency for closely related species to exhibit more similar phenotypes than more distantly related species, a pattern that often reflects shared ancestry and historical evolutionary processes (Blomberg and Garland, 2002; Losos, 2008). Complementary indices such as Pagel's $\lambda$ and Blomberg's K, together with autocorrelation metrics (Moran's I, Abouheif's $C_{mean}$), allow testing under differing evolutionary assumptions. Moreover, recently developed ordination techniques like phylogenetic principal component analysis (pPCA) permit statistically robust treatment of high-dimensional functional trait matrices (Revell, 2009; Adams, 2014). The pPCA graphically summarizes the phylogenetic relationships within a complex set of functional trait variables. The first principal component corresponds to the highest eigenvalue, representing large variance with strong positive autocorrelation (Jombart et al., 2010). These methods are particularly well-suited to macrobenthic communities where morphology, life history, and reproductive strategies jointly determine its ecological roles.

Mathematically, PS reflects the statistical dependence between traits and the phylogenetic tree under a given model of evolution. Multiple evolutionary processes can generate similar PS patterns that limit the ability to infer specific mechanisms (Losos, 2008; Ackerly, 2009). To overcome these limitations, phylogenetic comparative methods help to identify evolutionary patterns in species' traits, offering insight into the processes that shape niche evolution (Blomberg and Garland, 2002; Cooper et al., 2010; Harmon et al., 2010; Münkemüller et al., 2012). The classical Brownian Motion (BM) model assumes trait covariance is proportional to shared ancestry (Felsenstein, 1973), but it has been extended to incorporate ecological and evolutionary complexities (Pagel, 1999). Among these, the Ornstein–Uhlenbeck (OU) model adds a parameter to represent stabilizing selection toward an adaptive optimum shared by a clade (Beaulieu et al., 2012; Cooper et al., 2016) and modeling environmental constraints that limit trait evolution. Conversely, the Early Burst (EB) model describes rapid phenotypic diversification early in clade history, with evolutionary rates decelerating over time (Harmon et al., 2010). Because evolution simultaneously shapes multiple traits; hence, multivariate comparative methods are essential to capture clade-level phenotypic evolution (Clavel et al., 2015). The presence of PS can indicate patterns of niche conservatism where closely related species retain similar ecological roles and can identify phylogenetic clustering of vulnerability to environmental changes (Cooper et al., 2010; Molina-Venegas and Rodríguez, 2017). Hence, combining PS measurements with evolutionary models thus provides powerful tools to study phylogenetic niche conservatism and the evolutionary forces in shaping biodiversity.

To date, several studies have focused primarily on macrobenthic taxonomic diversity from Arctic fjords (Kędra et al., 2010; Bodil et al., 2011; Pawłowska et al., 2011; Włodarska-Kowalczuk et al., 2012; Legeżyńska et al., 2017; Molis et al., 2019; Kokarev et al., 2021; Molina, 2023) without explicitly examining phylogenetic constraints on functional trait distributions. Trait-based analyses of macrobenthic organisms have also been recently applied in several Arctic regions, including those in the Barents Sea, Chukchi Sea, Laptev Sea, and Canadian Arctic (Cochrane et al., 2012; Krumhansl et al., 2016; Kokarev et al., 2017; Rand et al., 2018; Liu et al., 2019; Käß et al., 2021). However, none of these studies have incorporated phylogenetic relationships to understand evolutionary constraints on trait evolution. Arctic fjords are characterized by unique selective pressures, including extreme seasonality, episodic organic matter inputs, and rapid regional warming. Considering these selective pressures prevalent in this eco-region, it is essential to determine whether trait variation is largely constrained by phylogeny or reflects ecological flexibility. This knowledge may be vital for predicting the resilience of benthic communities in the face of ongoing Atlantification and glacier retreat.

In recent years, mitochondrial genomes, particularly the mitochondrial cytochrome *c* oxidase subunit I (mtCOI) gene, are widely used for species identification and phylogenetic analysis (Bhaumik and Mandal, 2024). The mtCOI region offers high taxonomic resolution due to rapid evolution and conserved priming sites, enabling broad amplification in diverse macrobenthic groups suitable for phylogenetic studies (Christodoulou et al., 2025). Its broad taxonomic coverage and extensive representation in available databases make it particularly suitable for phylogenetic and trait-based comparative analyses (Ratnasingham and Hebert, 2007). Against this backdrop, this study is a novel attempt to integrate DNA-barcode phylogenies (mtCOI) with functional traits in macrobenthic assemblages from the Kongsfjorden–Krossfjorden system, Svalbard. By combining these data, we aim to elucidate the evolutionary dynamics through PS analysis and evolutionary models of trait evolution. The present study aims to: (1) quantify PS across 21 functional traits by applying complementary univariate and multivariate metrics (Pagel's $\lambda$, Blomberg's K, Moran's I, Abouheif's $C_{mean}$) and by mapping local phylogenetic autocorrelation to detect clade-level patterns; (2) characterize multivariate phylo-functional structure by reconstructing an mtCOI-based phylogeny for 50 species, performing pPCA to extract dominant phylo-functional axes, and deriving a composite phylogenetic primary-axis species score (PPASS) that summarizes major trait variation while accounting for shared ancestry; and (3) evaluate the evolutionary processes that shape functional trait variation in Arctic macrobenthos by fitting and comparing evolutionary models of trait evolution (BM, OU and EB).

## 2. Materials and methods

### 2.1. Study area

Kongsfjorden, an open glacial fjord located near Ny-Ålesund on the western coast of Svalbard, extends approximately 20 km in length and 4–10 km in width (MacLachlan et al., 2010). Its outer region is shaped by the interaction between warm Atlantic and cold Arctic water masses (Cottier et al., 2005), while glacial meltwater and sediment inputs create pronounced environmental gradients toward the inner fjord (Hop et al., 2002; Tripathy et al., 2023). These meltwater inputs generate strong gradients in salinity, temperature, sedimentation, and particle composition along the fjord (Svendsen et al., 2002; Kuliński et al., 2014). The inner fjord is characterized by unstable, frequently resuspended sediments, while the outer regions contain more stable muddy substrates (Dowdeswell, 1987; Włodarska-Kowalczuk and Pearson, 2004). To the north, Krossfjorden forms a connected fjordic system with Kongsfjorden, known as the Kongsfjorden–Krossfjorden system (78°50′–79°30′ N, 11°–13° E), which opens into the deep glacial basin of

Kongsfjordenrenna (Saraswat et al., 2018). Kongsfjorden, the southern arm, is oriented southeast–northwest, whereas Krossfjorden, the northern arm, is aligned north–south (Svendsen et al., 2002).

The hydrographic and depositional gradients along the Kongsfjorden–Krossfjorden system are well documented and are known to be sensitive to benthic communities residing in these fjords (Kędra et al., 2010, 2012; Legeżyńska et al., 2017; Molis et al., 2019). This makes the area an ideal natural laboratory for studying the PS and functional ecology of Arctic macrobenthos. The coexistence of Atlantic- and Arctic-influenced waters creates sharp hydrographic contrasts (Cottier et al., 2005), while intense sediment input and fjord-specific hydrodynamics structure distinct benthic habitats (MacLachlan et al., 2010; Saraswat et al., 2018). Combined with observed macrobenthic responses to these drivers, the system's sensitivity to water-mass variability and glacial forcing further renders it especially well-suited for examining evolutionary patterns and climate-driven ecosystem changes in high-latitude benthic assemblages (Sagan and Darecki, 2018; Hop and Wiencke, 2019).

### 2.2. Sample collection

In June–July 2023, sediment samples were obtained from 13 stations comprising six sites in Kongsfjorden, five in Krossfjorden, and two in the adjoining open ocean (Fig. 1). Sampling was conducted using a Van Veen grab, and the collected material was immediately washed on-board through a 0.5 mm mesh sieve to retain macrobenthic organisms. Precaution was taken throughout to minimise damage to fragile specimens. The retained fraction was fixed in 70 % ethanol for subsequent morphological and molecular examination.

In the laboratory, specimens were sorted and identified to the lowest possible taxonomic level using a stereo-zoom microscope and a compound microscope fitted with an imaging system, following established identification keys and monographs (Fauvel, 1953; Day, 1967; Gagaev, 2009; Bodil et al., 2011; Dnestrovskaya and Jirkov, 2012). High-resolution photographs of voucher specimens were taken using an Olympus SZX7 stereoscope and a Nikon ECLIPSE Ci compound microscope. A total of 50 macrobenthic species were collected from the study stations. Details of the species names and collected location have been provided in Supplementary Table 1. Taxonomic nomenclature was verified against authoritative online databases, including the World Register of Marine Species (WoRMS; https://www.marinespecies.org), Arctic Register of Marine Species (ARMS; http://www.marinespecies.org/arms), and the Integrated Taxonomic Information System (ITIS; https://www.itis.gov).

### 2.3. Macrobenthic functional traits

A total of 21 functional traits, classified into six categories, were selected to investigate the evolutionary diversification of these traits across the macrobenthic phylogeny in the two Arctic fjords (Table 1). Information regarding the functional traits of each macrobenthic species identified from the study area were mined from published literatures (Bremner et al., 2003, 2006; Cochrane et al., 2012; Darr et al., 2014; Krumhansl et al., 2016; Kokarev et al., 2017; Rand et al., 2018; Bhaumik et al., 2023), various online websites like Polytraits (Faulwetter et al., 2014), The Arctic Traits Database (Degen and Faulwetter, 2019) and Biological Traits Information Catalogue (BIOTIC) (Marshall et al., 2006). Fuzzy coding principles (Chevene et al., 1994) were employed to

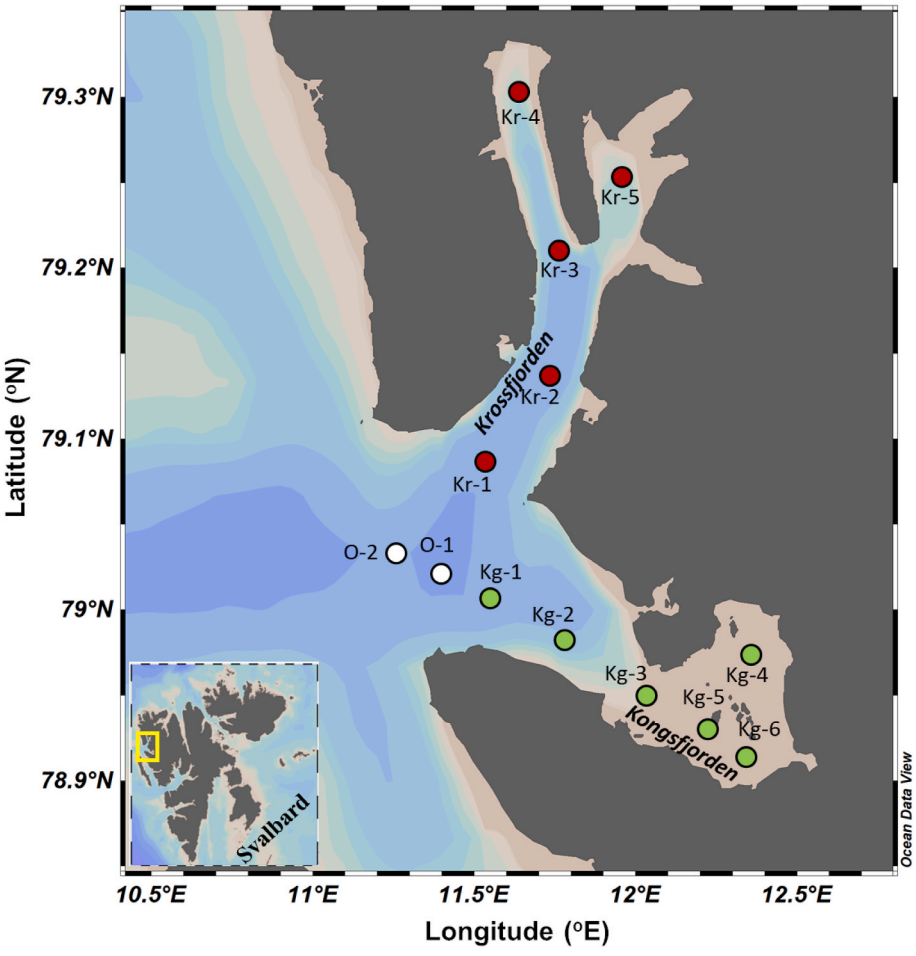



**Fig. 1.** Map showing the sampling locations in the high Arctic fjords. All sampling stations are marked with station numbers.

**Table 1**
Measures of PS and associated *p*-values for each of 21 macrobenthic functional trait category.
Abbreviations: $C_{mean}$ = Abouheif's $C_{mean}$; I = Moran's I; K = Blomberg's K; $\lambda$ = Pagel's lambda.

| Trait (Abbreviations) | Categories | Cmean | *p*-value | I | *p*-value | K | *p*-value | $\lambda$ | *p*-value |
|---|---|---|---|---|---|---|---|---|---|
| Body size (BS) | Small (Sm) (<3 cm) | 0.216 | **0.010** | 0.028 | 0.077 | 0.784 | **0.003** | 2.760 | **0.001** |
| | Medium (Me) (3–6 cm) | 0.108 | 0.079 | 0.010 | 0.197 | 0.580 | 0.076 | 3.079 | **0.001** |
| | Large (La) (>6 cm) | 0.277 | **0.004** | 0.042 | 0.043 | 0.717 | **0.010** | 3.237 | **0.001** |
| Motility (M) | Motile (Mo) | 0.098 | 0.123 | 0.006 | 0.207 | 0.544 | 0.183 | 2.681 | **0.001** |
| | Discretely motile (DM) | 0.191 | **0.025** | 0.037 | 0.094 | 0.593 | 0.061 | 1.000 | **0.001** |
| | Sessile (Se) | 0.100 | 0.127 | −0.005 | 0.205 | 0.566 | 0.182 | 0.000 | 1.000 |
| Living habitat (LH) | Tube dweller (Tu) | 0.310 | **0.002** | 0.013 | 0.054 | 0.691 | **0.023** | 1.000 | **0.001** |
| | Burrower (Bu) | 0.226 | **0.010** | 0.053 | **0.004** | 0.701 | **0.008** | 1.000 | **0.001** |
| | Free swimmer (FS) | 0.212 | **0.027** | 0.009 | 0.055 | 0.710 | **0.021** | 2.719 | **0.001** |
| | Crawler (Cr) | 0.317 | **0.002** | 0.138 | **0.016** | 0.002 | 0.573 | 2.391 | **0.001** |
| | Attached (At) | −0.011 | 0.310 | −0.039 | 0.833 | 0.000 | 0.836 | 2.175 | **0.001** |
| Feeding strategy (F) | Sub surface deposit feeder (SSDF) | 0.277 | **0.002** | 0.013 | 0.097 | 0.739 | **0.007** | 0.683 | **0.049** |
| | Surface deposit feeder (SDF) | −0.021 | 0.502 | 0.059 | **0.011** | 0.528 | 0.175 | 2.505 | **0.001** |
| | Suspension feeder (SF) | 0.187 | **0.030** | 0.005 | 0.108 | 0.716 | **0.012** | 2.403 | **0.001** |
| | Carnivore (Car) | 0.225 | **0.012** | 0.003 | 0.090 | 0.525 | 0.292 | 2.200 | **0.001** |
| | Scavenger (Sca) | 0.229 | **0.010** | 0.005 | 0.106 | 0.513 | 0.354 | 3.229 | **0.001** |
| Environmental position (EP) | Epifaunal (Epi) | 0.498 | **0.001** | 0.161 | **0.001** | 1.302 | **0.001** | 2.146 | **0.001** |
| | Infaunal (In) | 0.519 | **0.001** | 0.176 | **0.001** | 1.326 | **0.001** | 2.192 | **0.001** |
| Reproductive strategy (RS) | Asexual (A) | 0.061 | 0.101 | −0.016 | 0.209 | 0.555 | 0.313 | 1.177 | **0.002** |
| | Sexual brooder (SB) | 0.235 | **0.014** | 0.007 | 0.089 | 0.634 | 0.056 | 1.000 | **0.001** |
| | Sexual spawner (SS) | 0.282 | **0.005** | 0.006 | 0.075 | 0.684 | **0.028** | 1.177 | **0.001** |

assign scores to each trait for individual taxa. A scale ranging from 0 to 3 was used, where obligate and total affinity traits were scored as 3, while non-affinity traits received a score of 0. For taxa exhibiting multiple traits within a single category, scores of 1 or 2 were assigned based on their affinity towards each specific trait relevant to the species' life history. In instances where trait information for specific genera or species was lacking, trait data from other species within the same family were used as proxies (Rand et al., 2018). To eliminate bias between different trait modalities, the affinity scores for each trait were standardized such that their sum equalled 1 (Darr et al., 2014). For instance, if a macrobenthic species exhibits both carnivorous and scavenging feeding habits but primarily consumes live animals, the affinity scores for "Carnivore" and "Scavenger" were assigned as 3 and 1, respectively, resulting in standardized values of 0.75 and 0.25 (Chevene et al., 1994). Fuzzy traits were normalised using prep. fuzzy function from 'ade4' package in R.

### 2.4. DNA extraction and PCR reactions

Following morphological identification representative individuals of each morphologically identified species were subjected to DNA barcoding to confirm species identity. Genomic DNA was extracted from samples using the QIAGEN DNeasy Blood and Tissue Kit, following the manufacturer's protocol. The mtCOI gene region was amplified using the universal primer pair LCO1490 and HCO2198 (Folmer et al., 1994). PCR reactions were prepared following standard protocols (Bhaumik et al., 2025b), using 50–100 ng template DNA, 1 × buffer, 2.5 mM $MgCl_2$, 0.2 mM dNTPs, 10 μM of each primer and Taq polymerase. Amplification involved an initial denaturation at 94 °C, followed by 30 cycles of denaturation, annealing, extension, and a final elongation at 72 °C (Bhaumik and Mandal, 2024). The PCR products were separated on 2 % ethidium bromide stained agarose gels, purified with the QIAquick Gel Purification Kit, and bidirectionally Sanger sequenced using the same primers. Sequencing was successful for all species except *Leitoscoloplos mammosus* for which mtCOI sequences were retrieved from the BOLD database. This additional sequence was incorporated to support phylogenetic analyses of the complete dataset, encompassing all 50 macrobenthic species sampled from the study area.

## 3. Data analysis

The mtCOI sequences were edited in BIOEDIT (v 7.2.6; Hall, 1999), aligned using CLUSTAL W (Thompson et al., 1994), and verified against GenBank records (Altschul et al., 1990). Validated sequences were deposited in NCBI GenBank (Supplementary Table 1). All mtCOI sequences for the 50 macrobenthic species were compiled in MEGA X (Kumar et al., 2018) and aligned using the MUSCLE algorithm (Edgar, 2004). We used both corrected Akaike Information Criterion (AICc) and Bayesian Information Criterion (BIC) to enhance statistical rigor for phylogenetic model selection (Schwarz, 1978). Model testing in MEGA X identified GTR+G+I as the best-fit model, based on the lowest AICc (42968.577) and BIC (43881.997) values. Phylogenetic analysis was performed using the maximum likelihood method with the GTR + G + I nucleotide substitution model and 1000 bootstrap replicates (Rodríguez et al., 1990). The phylogenetic tree was rooted using the chordate *Styela rustica* as an outgroup to the 50 non-chordate species analyzed; however, this taxon was excluded from subsequent trait analyses.

The phylogenetic tree constructed in MEGA X and the trait data frame were then combined into a *phylo4d* object using the constructor function *phylo4d* from the "phylobase" package in R. Pairwise phylogenetic proximities between the tips of the tree were calculated using the *proxTips* function from the "adephylo" R package. It defines phylogenetic proximities as a function of phylogenetic distances, with higher values indicating greater contrasts between taxa. Among the different phylogenetic distance types available, patristic distance and nNodes distance were computed. These distances were considered due to their biological relevance, as the patristic method represents the amount of evolutionary change separating two taxa, while the nNodes method measures the number of speciation events.

The PS captures proportional variation in traits as a function of phylogenetic distances. It is a proxy for shared evolutionary history and prevalence of common ancestry after repeated evolutionary processes (Blomberg and Garland, 2002; Losos, 2008). The PS indices, their associated statistical tests, and graphical visualisations were calculated using the "phylosignal" package in R (Keck et al., 2016). PS for each biological trait was computed using standard indices like Pagel's $\lambda$ (Pagel, 1999), Blomberg's K (Blomberg et al., 2003), Moran's I, and Abouheif's $C_{mean}$ (Münkemüller et al., 2012). Values of $\lambda$, K, I, and $C_{mean}$ greater than zero indicate significant relationships between traits and phylogeny. Pagel's $\lambda$ and Blomberg's K both assume a Brownian-motion (random drift) model of trait evolution, whereas $C_{mean}$ and Moran's I are autocorrelation indices independent of any specific evolutionary model.

To visualize PS patterns, phylogenetic correlograms based on Moran's I were generated using the "phylosignal" package in R (Hardy and

Pavoine, 2012). These correlograms display autocorrelation among traits with increasing phylogenetic distances (Sokal and Oden, 1978). Positive autocorrelation occurs when closely related species share similar trait values, whereas strong contrasts between sister taxa indicate negative autocorrelation. Confidence intervals were obtained via non-parametric bootstrap resampling (Keck et al., 2016). While global PS metrics assume uniform trait evolution across the tree, local variations are also commonly observed. Therefore, Local Indicators of Phylogenetic Association (LIPA), based on the local Moran's I ($I_i$) metric, were used to identify clades showing particularly strong autocorrelation (Keck et al., 2016).

A pPCA was performed using the *ppca* function in the "adephylo" R package (Jombart and Dray, 2010) on centred and scaled trait data for 21 biological traits from 50 macrobenthic species sampled in Arctic fjords. Since phylogenetic principal components typically have reduced variance compared to non-phylogenetic PCAs, it reduces type I errors when used in subsequent phylogenetic analyses (Revell, 2009).

To summarise trait variation while accounting for phylogeny, a composite metric, phylogenetic primary-axis species score (PPASS) was derived from the first axis of the pPCA, capturing the maximum variance in traits influenced by phylogeny for each species. Furthermore, each species was classified based of four larval development strategy (Planktotrophic, Lecithotrophic, Direct and Mixed). Since trait variation is not phylogenetically independent, phylogenetic generalised least squares (PGLS) models were fitted using the caper R package (Orme et al., 2018), with PPASS as the dependent variable and method of larval development as the predictor. Pagel's $\lambda$ was estimated in the PGLS models via maximum likelihood. Statistical analyses were performed in the R environment (R Core Team, 2024).

To investigate the evolutionary dynamics of macrobenthic functional traits, we tested whether their evolution followed Brownian Motion (BM), Early Burst (EB), or Ornstein–Uhlenbeck (OU) models. Prior to analyses, phylogenetic polytomies were resolved using the 'multi2di' function of the 'ape' R package (Paradis and Schliep, 2019), and the tree was transformed into an ultrametric form with the 'force.ultrametric' function from 'phytools' (Revell, 2012). Models were fitted across the full phylogeny under the assumption of a single selective regime per trait, with OU models constrained to one adaptive optimum. Model performance was evaluated based on log-likelihood and the small-sample corrected Akaike Information Criterion (AICc), considering models within two AICc units of the best fit as having comparable support (Burnham and Anderson, 2002). Multivariate evolutionary patterns were assessed using the 'mvMORPH' R package (Clavel et al., 2015), while univariate model fitting employed 'geiger' (Pennell et al., 2014). Trait evolution was visualized by mapping trait values onto the phylogeny using the 'contMap' function in 'phytools' (Revell, 2012).

## 4. Results

### 4.1. Multi-trait structure

The *phylo4d* plot reveals strong phylogenetic clustering of key traits among Arctic macrobenthos (Fig. 2). Bivalves like *Yoldia hyperborea*, *Yoldiella lenticula*, *Axinopsida orbiculata*, and *Ennucula tenuis* consistently display large body size, burrowing living habitat, high motility, and deposit feeding. Polychaetes such as *Maldane sarsi*, *Leitoscoloplos mammosus*, and *Lagis koreni* group by small to medium body size, tube/burrow dwelling, motility, and deposit feeding. Ophiuroids like *Ophiura robusta* and *Ophiocten gracilis* cluster for carnivory or omnivory and free-swimming or crawling habitats. In contrast, reproductive strategies and some body size classes are distributed across the phylogeny, reflecting lability. Overall, feeding habitat and motility show strong PS, while reproductive traits and body size are more evolutionarily flexible.

### 4.2. Phylogenetic distances

Pairwise phylogenetic distances among the 50 Arctic macrobenthic species, calculated using both patristic (Fig. 3a) and nNodes distance (Fig. 3b), consistently demonstrate strong evolutionary structuring. Across both metrics, closely related species such as *Leitoscoloplos mammosus* and *Lagis koreni* or *Yoldiella lenticula* and *Ennucula tenuis* show low nNodes distances ($\leq$0.05–0.10), indicating high phylogenetic proximity. In contrast, nNodes distances reach as high as 1.0 between taxonomically distant groups such as polychaetes and bivalves (*Leitoscoloplos mammosus* and *Axinopsida orbiculata*), reflecting deep evolutionary separation. Patristic distances show similar patterns, with minimal branch separation within major clades and marked divergence between functional groups like bivalves and cirripeds or echinoderms. The use of both metrics together ensures robust detection of PS and clade-level conservation of traits, with within-clade distances as low as 0.05 and between-clade distances up to 1.0, confirming strong evolutionary cohesion and marked divergence in Arctic macrobenthic assemblages.

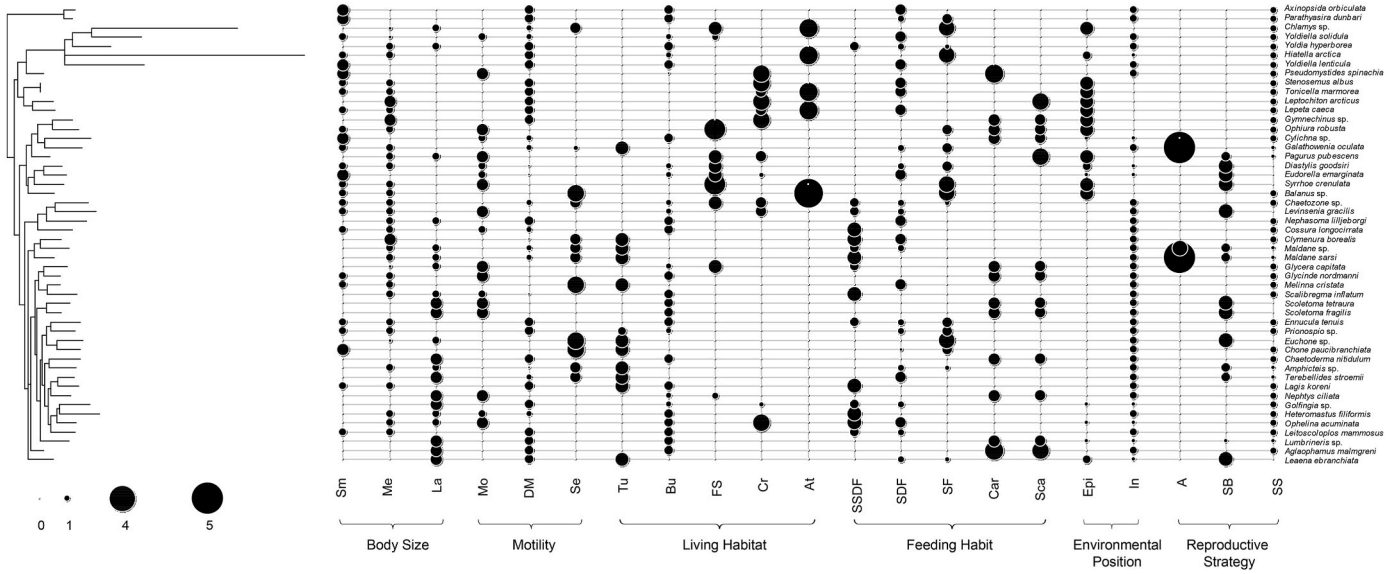



**Fig. 2.** *Phylo4d* plot of functional traits along with mtCOI-based phylogeny of 50 macrobenthic species from high Arctic fjords.

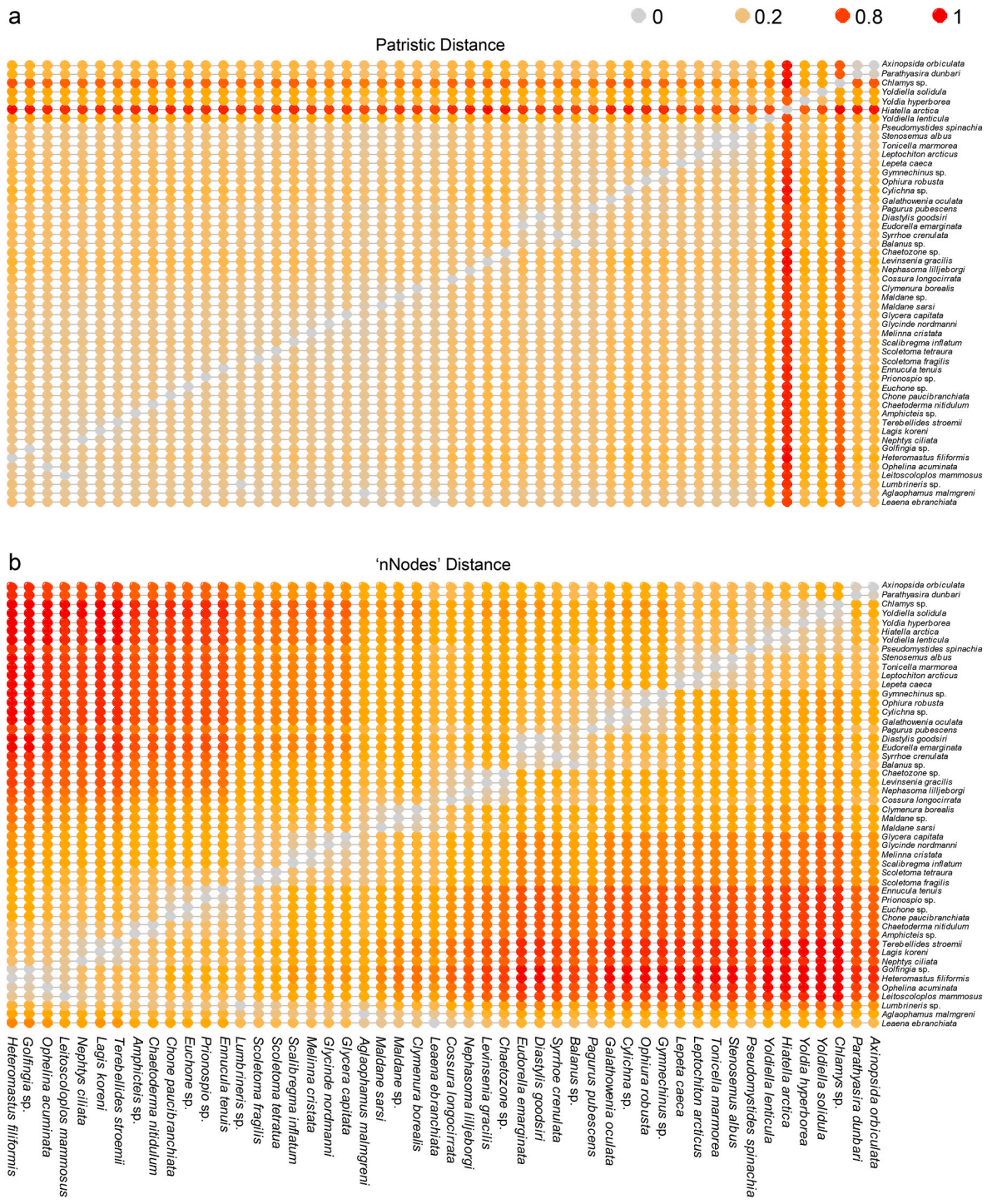



**Fig. 3.** Pairwise phylogenetic distances among the Arctic macrobenthic species using (a) patristic distance and (b) nNodes distance.

### 4.3. Phylogenetic signal

The PS analyses revealed strong and significant structuring for multiple functional traits (Table 1). Pagel's $\lambda$ was high ($\geq$1.0, $p = 0.001$) for almost all traits, indicating strong evolutionary conservatism. Blomberg's K also supported high PS ($K \geq 0.68$, $p < 0.05$) for traits 'Bu' (Burrower), 'FS' (Free swimmer), 'SSDF' (Sub surface deposit feeder), 'SF' (Suspension feeder), 'SS' (Sexual spawner), and 'La' (Large). Autocorrelation metrics confirmed these patterns: Abouheif's $C_{mean}$ was highest and significant for 'Cr' (Crawler; 0.317, $p = 0.002$), 'Tu' (0.310, $p = 0.002$), 'La' (0.277, $p = 0.004$), and 'SSDF' (0.277, $p = 0.002$) while Moran's I detected strong phylogenetic clustering for traits 'Bu' (0.053, $p = 0.004$), 'SDF' (Surface deposit feeder; 0.059, $p = 0.011$), 'Cr' (0.138, $p = 0.016$), 'Epi' (Epifaunal) and 'In' (Infaunal) both >0.16, $p = 0.001$. Traits such as 'Sm' (Small), 'Me' (Medium), 'DM' (Discretely motile), and 'A' (Asexual) showed low or non-significant PS in most metrics ($p >$ 0.1), suggesting evolutionary lability or convergence. Some traits had negative or near-zero $C_{mean}$ values, indicating little to no phylogenetic autocorrelation. Trait 'At' (Attached) showed a slightly negative and non-significant $C_{mean}$ (−0.011, $p = 0.31$), implying slight phylogenetic structuring.

Phylogenetic autocorrelation in functional traits was assessed using

both global Moran's I and local Moran's $I_i$ (LIPA) analyses to capture trait clustering across Arctic macrobenthic assemblages. To uncover finer-scale evolutionary patterns, local Moran's *Ii* values were used to detect clade-level trait clustering (Fig. 4). Highly significant local autocorrelation was detected for trait 'Tu' in *Euchone* sp. ($p = 0.001$), *Chone paucibranchiata* ($p = 0.001$), *Maldane sarsi* ($p = 0.002$), *Maldane* sp. ($p = 0.002$), *Clymenura borealis* ($p = 0.002$), *Lagis koreni* ($p = 0.003$), and *Terebellides stroemi* ($p = 0.004$). For 'Bu', significant local clustering was observed in *Tonicella marmorea* and *Stenosemus albus* (both $p = 0.001$), *Lepeta caeca* and *Leptochiton arcticus* (both $p = 0.013$), and *Gymnechinus* sp. ($p = 0.019$). 'La' showed significant local autocorrelation in multiple polychaete species, including *Aglaophamus malmgreni*, *Lumbrinereis* sp., *Nephtys ciliata*, *Golfingia* sp., and both *Scoletoma* species (all $p = 0.001$). Significant autocorrelation was exhibited by 'Sm' trait in *Ophelina acuminata*, *Heteromastus filiformis*, *Amphicteis* sp., *Golfingia* sp., and both *Scoletoma* species (all $p \leq 0.004$). In contrast, traits such as 'Me', 'DM', 'A' displayed non-significant local autocorrelation values (most $p > 0.1$), reflecting evolutionary lability and limited phylogenetic constraint (Fig. 4). The integration of global and local Moran's analyses demonstrates that pronounced phylogenetic clustering for substrate use, feeding strategies, and body size is concentrated within specific evolutionary lineages, while other functional traits remain evolutionarily flexible across Arctic macrobenthic phylogeny.

### 4.4. Phylogenetic correlogram analysis

Phylogenetic correlograms revealed distinct distance-dependent autocorrelation patterns across functional traits, providing insights into evolutionary constraints that shape Arctic macrobenthic assemblages. Body size traits showed different phylogenetic structures. 'Sm' showed strong positive autocorrelation at short phylogenetic distances followed by a rapid decline. This implies closely related species share small body size, but the constraint weakens with phylogenetic distance. 'La' exhibited moderate positive autocorrelation at intermediate distances with significant clustering, which suggests episodic evolution of large-bodied forms in specific clades. 'Me' lacked a clear phylogenetic pattern, reflecting evolutionary flexibility in this size category (Fig. 5a–c).

Motility traits generally showed limited phylogenetic constraint. The 'Mo' (Motile) and 'Se' (Sessile) traits exhibited minimal autocorrelation across all distances, showing that these strategies evolved mostly independent of phylogeny (Fig. 5d and f). The 'DM' trait displayed moderate positive autocorrelation only at short distances, which points to some clustering among close relatives followed by rapid divergence at greater distances (Fig. 5e).

Living habitat traits revealed the strongest phylogenetic signals. The 'Tu' trait exhibited exceptionally strong positive autocorrelation across all distances with extensive significant clustering. This pattern is likely due to deep evolutionary conservatism in tube-dwelling architecture. The 'Bu' trait showed strong positive autocorrelation at short distances with rapid decay and mixed clustering. This suggests burrowing habits are conserved within lineages but have evolved independently multiple times. 'Cr' showed persistent positive autocorrelation at intermediate distances with significant clustering. This reflects conservatism in epibenthic mobility. In contrast, 'At' had weak negative autocorrelation, which implies highly labile evolution of attachment strategies (Fig. 5g–k).

Feeding strategies displayed variable phylogenetic structure. The 'SSDF' trait showed moderate positive autocorrelation at short distances, which indicates some phylogenetic clustering within clades. The 'SDF' and 'SF' traits showed minimal phylogenetic structure, suggesting convergent evolution. The 'Car' (Carnivore) trait exhibited significant positive autocorrelation only at the maximum phylogenetic distance which depicts deep evolutionary constraints on predatory strategies. The 'Sca' (Scavenger) trait showed extensive significant clustering across multiple distances, reflecting phylogenetic conservatism in detrital feeding (Fig. 5l–p).

Environmental position traits 'Epi' and 'In' exhibited the most

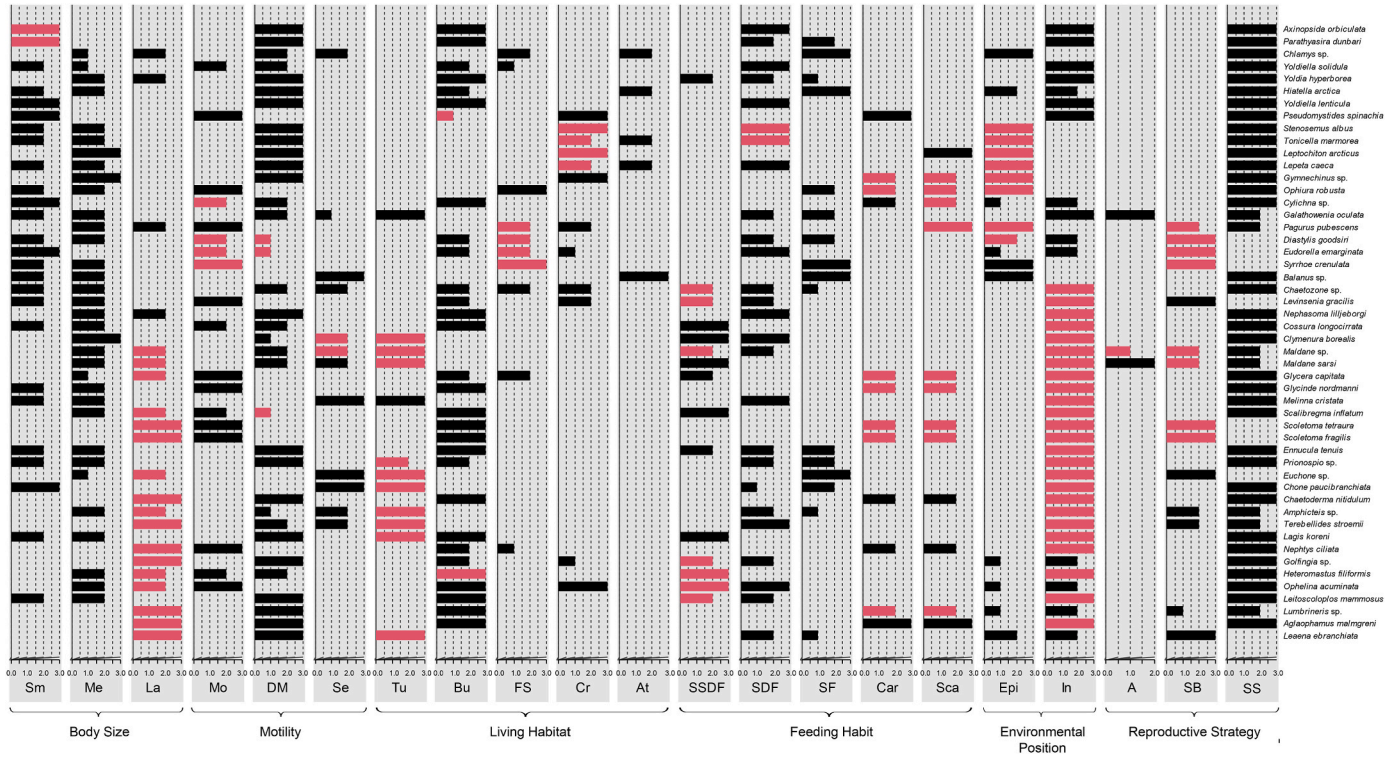



**Fig. 4.** Barplot of local Moran's index ($I_i$) values for each macrobenthic species and trait categories. The value of $I_i$ denotes (black bars) the degree of autocorrelation between closely related species and red bars denote statistically significant ($p$-value <0.05) $I_i$ values. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

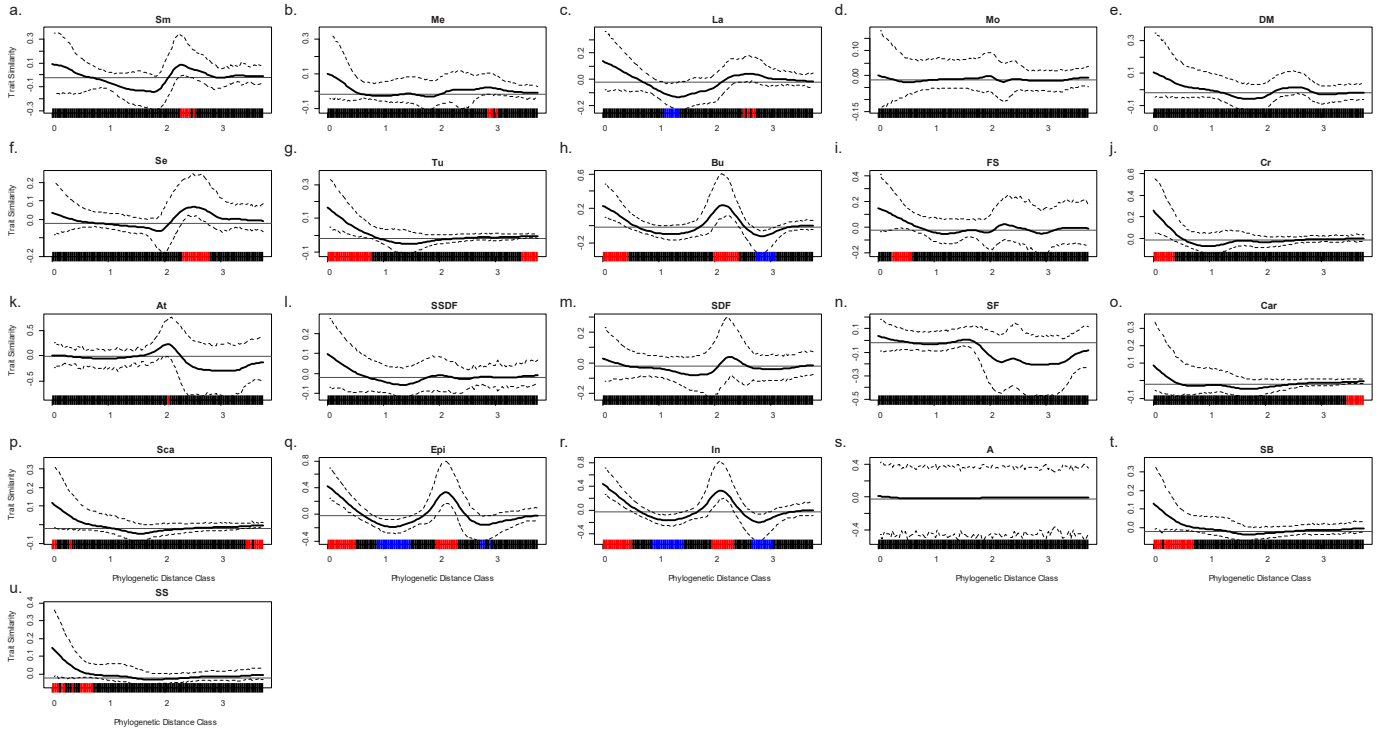



**Fig. 5.** Phylogenetic correlograms for Arctic macrobenthic functional traits (a–c) body size (d–f) motility (g–k) living habitat (l–p) feeding habit (q–r) environmental position (s–u) reproductive strategy. The solid line is Moran's I autocorrelation metric and dashed black lines are the lower and upper limits of the confidence interval (95 % confidence). The horizontal black line denotes expected value of Moran's I under the null hypothesis of no phylogenetic autocorrelation. A red-coloured bar denotes significant positive autocorrelation, while a blue-coloured bar denotes significant negative autocorrelation. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

pronounced phylogenetic structure. Both traits demonstrated sustained positive autocorrelation and extensive significant clustering across multiple distances. This pattern suggests that episodic life history strategies represent deeply conserved trait complexes maintained across major evolutionary divergences (Fig. 5q–r). By contrast, reproductive traits showed minimal phylogenetic constraint. Asexual reproduction exhibited nearly flat correlograms across all distances, demonstrating complete phylogenetic independence. The 'SB' (Sexual brooder) and 'SS' traits showed weak positive autocorrelation only at short distances. This pattern connotes these reproductive modes are phylogenetically labile and evolve rapidly in response to environmental pressures (Fig. 5s–u). Overall, the correlograms reveal a hierarchical pattern of evolutionary constraint. Living habitat traits show the strongest phylogenetic conservatism, feeding habits demonstrate intermediate constraint, while reproductive strategies exhibit the greatest evolutionary lability.

### 4.5. Phylogenetic principal component analysis (pPCA)

The pPCA on 21 morphological and ecological traits across 50 marine benthic invertebrate species revealed that the first principal component axis (PC1) captured the largest proportion of trait variance (Fig. 6). The PC1 explained 18.4 % of the total trait variation (eigenvalue 3.87), with substantial PS indicated by a Moran's I of 0.30. Most species clustered close to zero or positive PC1 values, representing a shared central trait tendency; notably, planktotrophic and benthic species were consistently found in this range. In contrast, molluscs with lecithotrophic mode of larval development strategy, *Stenosemus albus* and *Tonicella marmorea*, were identified as extreme outliers with highly negative PC1 scores (−4.66 and −4.33, respectively), which suggests distinct evolutionary divergence in their life-history strategies. The PPASS incorporated as a composite dependent variable in the PGLS model depicted trait variation as a response of larval development strategy across species [PGLS model = PPASS ~ Larval development; lambda (ML) = 0.96, kappa = 1.00, delta = 1.00, $R^2$adj = 0.0429, F (3,46) = 1.732]. Lecithotrophic development strategy was found to have a significant negative effect in the PGLS model ($p$ = 0.03492), driving the trait variation (Table 2a).

### 4.6. Models of trait evolution

Overall, multivariate functional trait evolution in Arctic macrobenthos was best explained by an Early Burst (EB) model, indicating an accelerated phase of early diversification followed by a deceleration in evolutionary rates (Table 2b). Similarly, the PPASS also followed the EB model as depicted by the lowest AICc value of 85.60 (Table 2b). Among univariate traits, all trait modalities of Body Size (Sm, Me, La) and motility (Mo, DM, Se) fitted by a Brownian Motion (BM) model, which implies gradual evolutionary change. Environmental position traits (Epi and In) were best explained by an EB model (Supplementary Table 2).

Feeding habit traits showed mixed model fits; 'Car' and 'Sca' followed the EB model, while 'SSDF', 'SDF', and 'SF' fit the BM model (Supplementary Table 2). All living habitat traits (Tu, Bu, FS, At) were best described by the BM model, except 'Cr', which fit the EB model. For reproductive strategies, 'A' and 'SS' were explained by the EB model, while SB followed the BM model (Supplementary Table 2). When trait evolution is visualized, traits that followed the EB model show greater diversification toward the root, while those explained by the BM model had a propensity to display greater diversification toward the terminal branches (Supplementary Fig. 1).

## 5. Discussion

### 5.1. Multi-trait phylogenetic clustering and phylogenetic distance variations

The *phylo4d* framework integrates phylogenetic trees along with trait




**Fig. 6.** Phylogenetic Principal Components Analysis of macrobenthic functional traitsfrom high Arctic fjords. Trait data was centred and scaled prior to PCA analysis. Positive and negative scores on PC1 are indicated by black and white circles, respectively. Symbol size is proportional to absolute values.

data to facilitate robust analysis of evolutionary patterns (Keck et al., 2016). Our analysis revealed a strong phylogenetic clustering among Arctic macrobenthic taxa. Polychaetes such as *Maldane sarsi*, *Leitoscoloplos mammosus*, *Lagis koreni* grouped together based on tube-dwelling and deposit-feeding traits. Similarly, large burrowing bivalves like *Yoldia hyperborea* and *Axinopsida orbiculata* formed distinct clades sharing deposit-feeding strategies. It underscores the evolutionary stability of sediment-dwelling life strategies that perform critical ecosystem functions like bioturbation and organic matter recycling (Kristensen et al., 2014; Zaborska et al., 2018; Udalov et al., 2021). This phylogenetic clustering of functionally similar species have been documented in other Arctic systems, where living habitat traits remain strongly conserved to maintain habitat stability and reduce predation risks in variable sedimentary environments (Al-Habahbeh et al., 2020; Pavlova et al., 2025).

Multi-trait clustering was strongly supported by phylogenetic distances, indicating clear evolutionary structuring within Arctic macrobenthos. Pairwise analyses using both nNodes and patristic distances showed closely related taxa consistently separated by low phylogenetic distances, while distant taxonomic relationships exhibited much greater separation. This evolutionary structuring provides the foundation for detecting PS in functional traits that has not been established for Arctic macrobenthic communities previously. Measuring both patristic

**Table 2**
(a) PGLS model predicting macrobenthic functional trait variation in Arctic fjords using Phylogenetic Primary Axis Species Score (PPASS) as the dependent variable and method of larval development as the predictor
(b) Comparisons of trait evolution models under Brownian Motion (BM), Early Burst (EB) and Ornstein Uhlenbeck (OU) approaches, for overall multivariate and PPASS data. Models are ranked according to their AICc values and denote differences between each pair of models relative to the most parsimonious model.

a.

| Variable | Estimate | Std. Error | t-value | *p*-value |
|---|---|---|---|---|
| Direct | −0.3804 | 0.47888 | −0.7944 | 0.43107 |
| Lecithotrophic | −1.04571 | 0.48109 | −2.1736 | **0.03492** |
| Mixed | −0.3651 | 0.469 | −0.7785 | 0.44028 |
| Planktotrophic | −0.40357 | 0.46722 | −0.8638 | 0.3922 |

b.

| Variable | Model | Log-likelihood | AIC | AICc |
|---|---|---|---|---|
| Multivariate dataset | **EB** | −971.9373 | 2449.875 | 2453.179 |
| | BM | −974.7895 | 2453.579 | 2459.928 |
| | OU | −974.7895 | 2453.579 | 2461.928 |
| pPCA (PPASS) | **EB** | −39.537883 | 85.075766 | 85.5975 |
| | BM | −63.610282 | 131.220564 | 131.4759 |
| | OU | −63.610282 | 133.220564 | 133.7423 |

distances (evolutionary change) and nNodes distances (speciation events) enables robust detection of phylogenetic clustering due to shared ancestry from convergent evolution (Blomberg et al., 2003; Thioulouse et al., 2018; Kallimanis et al., 2021).

### 5.2. Phylogenetic signal analysis of functional traits in Arctic macrobenthos

Pagel's $\lambda$ provides a quantitative measure of PS and ranges from 0 to 1. A $\lambda$ value of 0 indicates no phylogenetic influence, meaning that trait similarities between species are unrelated to their evolutionary relationships. Furthermore, a value of 1 indicates a strong PS consistent with the Brownian-motion model, where trait variation is fully explained by phylogeny. Intermediate values suggest a mixture of phylogenetic influence and other evolutionary processes (Pagel, 1999; Kamilar and Cooper, 2013). Building upon this phylogenetic foundation, our results revealed high and significant Pagel's $\lambda$ values ($\geq$1.0, $p$ = 0.001) for most of the traits, which indicates exceptionally strong PS. The strength of observed PS ($\lambda \geq 1.0$ for most traits) exceeds values typically reported for temperate marine invertebrates (Roman-Palacios et al., 2019; Zhang et al., 2025). It suggests that evolutionary history significantly constrains trait distributions within Arctic macrobenthic assemblages (Losos, 2008). This observed pattern in our study aligns closely with findings from Arctic marine systems, where macrobenthic communities exhibited strong phylogenetic structure in key functional traits such as body size, feeding mode, and habitat preferences (Liu et al., 2019; Zhulay et al., 2021). The pronounced PS observed for 'Tu' and 'Bu' reflects deep evolutionary conservatism for living habitat traits. These traits are recognised as essential for survival in Arctic fjord environments characterized by extreme seasonality and variable sediment dynamics (Zaborska et al., 2018; Udalov et al., 2021). According to Lento et al. (2023), Arctic stream macroinvertebrates exhibit strong phylogenetic conservatism for burrowing and tube-dwelling habits, which depicts evolutionary constraints on these habitat traits in extreme environments. Moreover, Blomberg's K varies from 0 to infinity, with K = 0 indicating phylogenetically independent trait evolution, K = 1 representing Brownian-motion evolution, and K > 1 denoting stronger-than-expected similarity among close relatives (Blomberg et al., 2003; Kamilar and Cooper, 2013). The exceptionally high Blomberg's K values ($\geq$0.68, $p < 0.05$) for feeding habit and environmental position observed in the present study surpass those typically reported for marine benthic invertebrates (Zhang et al., 2025). Significant PS was detected in feeding modes across marine invertebrate clades, emphasizing conservative evolution of these traits (Roman-Palacios et al., 2019). The strong PS in feeding modes likely reflect energy constraints in Arctic fjords, where low primary productivity and short phytoplankton bloom periods limits trophic diversification that may favor retention of ancestral feeding strategies (Zaborska et al., 2018; Udalov et al., 2021). Furthermore, low species richness with limited functional redundancy might reinforce stabilizing selection, and to maintain conserved feeding traits across macrobenthic lineages (Włodarska-Kowalczuk et al., 2012). Moran's I measure phylogenetic autocorrelation, with larger deviations from zero indicating stronger PS (Münkemüller et al., 2012). $C_{mean}$ measures the covariation of trait values relative to phylogenetic distance, with $C_{mean}$ = 1 and −1 indicating strong similarity among closely related taxa and strong negative associations correspondingly (Abouheif, 1999). High values for 'Cr' ($C_{mean}$ = 0.317, $p$ = 0.002) and 'Tu' ($C_{mean}$ = 0.310, $p$ = 0.002) behaviour obtained in our study are in accordance with the patterns observed in other Arctic benthic systems, where motility and habitat construction represent deeply conserved trait complexes (Włodarska-Kowalczuk et al., 2012; Voronkov et al., 2013).

The local Moran's index ($I_i$) revealed that phylogenetic clustering is concentrated within specific evolutionary lineages, particularly among tube-dwelling polychaetes (*Euchone* sp., *Chone paucibranchiata*, *Maldane sarsi*) and burrowing molluscs (*Tonicella marmorea*, *Stenosemus albus*). These results are consistent with studies on macrobenthic communities from Arctic fjords, which reported that tube-dwelling polychaetes like *Maldane sarsi* dominate inner-fjord fine-grained sediments (Pavlova et al., 2025). Burrowing molluscs such as *Tonicella marmorea* and *Stenosemus albus* persist in glacially influenced areas, reflecting lineage-specific adaptations to distinct sedimentary environments and hydrodynamic conditions (Al-Habahbeh et al., 2020). Local Moran's I ($I_i$) has been previously used to understand phylogenetic clustering of symbiotic bacterial lineages within coral reef invertebrates (O'Brien et al., 2021). Moreover, according to Martynov et al. (2020), multiple lineages of soft-substrate burrowing invertebrates evolve convergently within clades, thus supporting strong clade-specific habitat preferences. Our results have also portrayed that traits related to reproductive strategy (A, SB) and certain body size categories (Me) exhibited low or non-significant PS across most metrics ($p > 0.1$), indicating evolutionary lability. This pattern of phylogenetic independence in reproductive traits aligns with findings from other Arctic systems, where rapid environmental change has increased the lability of life history characteristics (Liu et al., 2019; Reed et al., 2021). Reed et al. (2021) documented significant reproductive plasticity in Arctic benthic invertebrates (*Astarte crenata* and *Ctenodiscus crispatus*) along the Barents Sea polar front. The above work depicted that reproductive traits remained flexible despite environmental gradients, where populations show episodic recruitment patterns linked to rapidly changing sea ice conditions and food availability. This reproductive lability allows Arctic species to respond to unpredictable environmental conditions rather than being constrained by their evolutionary history (Brandner et al., 2017). Similar patterns have been found in Arctic marine fish communities, where feeding and living habitat traits are phylogenetically conserved while life history traits show evolutionarily flexibility (Fossheim et al., 2015; Frainer et al., 2017). These findings represent the first quantification of PS in Arctic macrobenthic functional traits and demonstrate that evolutionary constraints play a crucial role in trait retention among Arctic taxa. While PS has been documented in various marine invertebrate groups globally (Roman-Palacios et al., 2019; Zhang et al., 2025), no studies have examined this phenomenon in Arctic macrobenthos.

### 5.3. Patterns of trait evolution from phylogenetic correlogram analysis

Phylogenetic correlograms are recently being applied to visualize evolutionary autocorrelation in community responses (Noonan et al., 2022; Tuya et al., 2024) and to detect conserved trait niches in diverse

taxa (Isobe et al., 2019; Tuya et al., 2024). Phylogenetic correlograms have been applied primarily to terrestrial plants (Hardy and Pavoine, 2012; Albassatneh et al., 2023), soil bacteria (Isobe et al., 2019), arbuscular mycorrhizal fungi (Roy et al., 2019). However, limited work has been conducted on freshwater (Heino and Tolonen, 2017) and marine communities (Tuya et al., 2024). By applying phylogenetic correlograms to Arctic macrobenthic communities, this study pioneers to unravel functional trait evolution across phylogenetic scales. The PS patterns were further elucidated through distance-dependent correlogram analyses that revealed hierarchical patterns of evolutionary constraint. According to our results, body size traits exhibited contrasting phylogenetic structures; 'Sm' showed strong positive autocorrelation at short phylogenetic distances with rapid decay, while 'La' displayed moderate positive autocorrelation at intermediate distances. This suggests body size evolution follows different evolutionary trajectories within Arctic benthos, with small-bodied forms representing a phylogenetically conserved strategy within closely related species, while large-bodied forms evolve episodically within specific clades. Morphological evolution commonly involves multiple rate shifts within clades, with some traits evolving rapidly while others undergo episodic changes (Puttick, 2018). Research showed small-bodied forms represent a strong PS within closely related fish genera, while maximum body size evolved more episodically and shows weaker phylogenetic constraint (Campbell, 2015). According to Klompmaker et al. (2015), an increase in large-bodied decapods is linked to new clade origins, with smaller sizes being conserved within lineages.

The phylogenetic correlogram results for motility traits show little phylogenetic constraint in 'Mo' and 'Se', which indicate that these strategies have evolved independently across species. Matz and Jürgens (2005) showed that high motility significantly reduces mortality in planktonic bacteria. According to the authors, motility strategies have evolved independently across diverse lineages, which explains the weak PS observed for 'Mo' and 'Se' traits. Conversely, 'DM' showed moderate autocorrelation at short phylogenetic distances, which suggests some retention of ancestral traits among closely related species but rapid divergence at larger scales. This pattern is common in traits related to locomotion, which often face strong ecological selection pressures due to evolutionary flexibility rather than strict phylogenetic conservatism (Collyer and Adams, 2018; Adams and Collyer, 2019). Philip et al. (2025) reported that losses of flagellar motility are clustered within specific clades. According to the authors, directed movement traits are conserved among close relatives but diverge rapidly across broader phylogenetic distances. Similar trends have been documented in marine benthic invertebrates, where motility trait adapts rapidly to local habitat conditions and predation (Beauchard et al., 2017). This flexibility likely helps Arctic macrobenthos respond to dynamic sediment and hydrodynamic conditions (Włodarska-Kowalczuk et al., 2012; Kiesel et al., 2020).

Trait 'Tu' exhibited exceptionally strong positive autocorrelation across all distance classes, indicating deep evolutionary conservatism that persists across major phylogenetic divisions (Włodarska-Kowalczuk et al., 2012; Glasby et al., 2021). According to this pattern, tube construction represents a fundamental plan that has been maintained throughout the evolutionary history of Arctic polychaetes. Researchers have demonstrated strong phylogenetic clustering of habitat-related strategies in benthic macroinvertebrates. Tube-dwelling trait is evolutionarily conserved across marine macroinvertebrate phylogenetic lineages as it provides adaptive advantages by reducing predation risk, hydrodynamic and sediment disturbance (Wang et al., 2021; Meijer et al., 2023). Its evolutionary persistence reflect strong constraints and habitat filtering which restricts trait divergence despite lineage diversification (Beauchard et al., 2017). Feeding strategies displayed variable phylogenetic structure, with 'SSDF' showing moderate positive autocorrelation at short distances that indicates phylogenetic clustering within clades but evolutionary divergence at greater phylogenetic distances. This pattern suggests feeding modes represent an intermediate level of evolutionary constraint, where phylogenetic history influences feeding strategies within families but ecological pressures drive convergent evolution across distantly related taxa (Beauchard et al., 2017). This is further supported by González-Trujillo et al. (2025), who reported that marine vertebrate communities worldwide show trophic convergence despite divergent evolutionary histories, indicating that similar environmental conditions can lead to the repeated evolution of analogous feeding strategies in unrelated lineages. The significant positive autocorrelation of the carnivory trait at maximum phylogenetic distance indicates deep evolutionary constraints of predatory strategies. This reflects specialized morphological and behavioral adaptations needed for successful hunting in Arctic environments (Włodarska-Kowalczuk et al., 2012). These findings are supported by empirical evidence from Antarctic marine ecosystems, which revealed a higher proportion of carnivorous and detritivorous feeding traits in Prydz Bay (Bhaumik et al., 2023). Organic-rich sediments from nearby Ice Shelf and glaciers have been found to promote the prevalence of predatory feeding behaviours in the Antarctic Bay, which may be consistent with Arctic fjords. According to Hu et al. (2019), the abundance of carnivores reflects healthier sediment conditions, which simultaneously allows diverse feeding strategies to flourish. Klobucar et al. (2021) found significant morphological divergence among Arctic Char populations linked to feeding ecology. Their results highlighted distinct body and jaw morphologies adapted to specific predatory strategies in Arctic marine ecosystems.

Environmental position traits (Epi, In) showed the most pronounced phylogenetic structure, with sustained positive autocorrelation across multiple distance classes and extensive significant clustering. Our result corroborates the work of Dumais et al. (2022), which exhibits strong spatial autocorrelation related to environmental gradient patterns in the benthic community of the Canadian Arctic Archipelago. It indicates that habitat utilization strategies represent deeply conserved trait complexes maintained across major evolutionary divergences. This result is consistent with findings from sub-Arctic communities that showed distinct spatial structures between epibenthic and infaunal sub-Arctic communities using Moran's eigenvector maps (Silberberger et al., 2019).

The phylogenetic correlogram results for reproductive traits showed minimal phylogenetic constraint. The 'A' trait exhibited a flat correlogram near zero across all phylogenetic distances, indicating phylogenetic independence. The 'SB' and 'SS' traits displayed weak positive autocorrelation at short phylogenetic distances, which indicates rapid evolution of these traits in response to environmental pressures. Similar patterns of low phylogenetic constraint and high evolutionary lability have been observed in both marine invertebrates and terrestrial organisms, where reproductive traits frequently evolve independently of phylogeny (Calatayud et al., 2016; Ibáñez et al., 2021). Phylogenetic independence of reproductive traits allows species to respond quickly to environmental variability, an important advantage in dynamic systems like Arctic fjords (Włodarska-Kowalczuk et al., 2012). These patterns highlight a balance between trait conservatism and diversification in Arctic environments, where environmental gradients from glacial inputs create strong selective pressures (Włodarska-Kowalczuk et al., 2012) while phylogenetic constraints limit evolutionary responses.

### 5.4. Phylogenetic principal component analysis of multivariate trait structure

The pPCA incorporates evolutionary relationships into multivariate ordination and provides a robust framework for analysing trait evolution (Revell, 2009). It addresses the statistical non-independence inherent in phylogenetic data (Jombart et al., 2010). The pPCA has been widely applied to study marine fish evolution; however, marine macrobenthos remain yet to be explored. The pPCA not only revealed morphological bursts in Carangarian fishes (Ribeiro et al., 2018) but also demonstrated elevated trait evolution in Haemulid speciation (Tavera

and Wainwright, 2019). Similarly, Davis and Betancur-R (2017) identified eco-morphological convergences across marine-freshwater transitions. The methodology has proven particularly valuable in marine systems where phylogenetic relationships strongly influence functional trait distributions (Collyer and Adams, 2021). Our pPCA result captured a significant amount of total trait variance with substantial PS (Moran's I = 0.30), which demonstrates the utility of this approach for phylogenetically structured data. The significant PS indicates that major axes of ecological differentiation among Arctic macrobenthic species are structured by evolutionary history. This pattern is consistent with other research finding, where closely related taxa tend to occupy similar positions in multivariate trait space that reflect shared evolutionary constraints and adaptive processes (Adams and Collyer, 2015). Highly negative PC1 scores observed in molluscs like *Stenosemus albus*, *Tonicella marmorea* with lecithotrophic mode of larval development demonstrates divergent evolutionary trajectories in life-history strategies within Arctic macrobenthic assemblages. These species represent evolutionary innovations in larval development that provide access to distinct ecological niches. Moreover, such specialized reproductive strategies are characteristic of polar marine invertebrates, where direct development and lecithotrophy have evolved as adaptive strategies to harsh environmental conditions and limited food availability (Barnes and Clarke, 2011; Reed et al., 2021). However, lecithotrophic larvae exhibit limited dispersal which reduces gene flow and constrains the spread of adaptive genetic variation necessary for functional trait diversification (Pascual et al., 2017). In accordance with this statement, our PGLS model further revealed lecithothrophic larval development strategy as a significant predictor which negatively influences macrobenthic trait variations in the Arctic fjords. According to Meyer-Kaiser et al. (2022) planktotrophic larval development dominates in Arctic fjords because as larvae with long pelagic durations can evade harsh conditions and disperse into suitable habitats as climate continues to warm. Furthermore, hydrodynamic complexity in Arctic fjords, characterized by variable circulation and stratification affects dispersal outcomes, leading to greater lability in dispersal modes among macrobenthic species (Descôteaux et al., 2022; Bhaumik et al., 2025a).

### 5.5. Evolutionary models for assessing trait diversification

Recently, evolutionary models have been extensively applied to understand trait diversification across various taxonomic groups (Pagel and Meade, 2025). These models demonstrate broad utility across marine organisms globally with applications ranging from the evolution of vertebrate swimming (Ferrón and Donoghue, 2022) to endotherm life history traits (Sol et al., 2025). However, evolutionary models have never been applied to Arctic macrobenthic communities, with most comparative-phylogenetic trait studies to date focusing on Antarctic notothenioid fishes (Colombo et al., 2015). A recent study by Sol et al. (2025) used OU models to study global marine endotherms, which revealed a critical geographic gap in model-based analyses of trait diversification in the high Arctic fjords. The present study represents the first application of comparative evolutionary models (BM, OU, EB) to understand trait evolution in macrobenthic communities from two high Arctic fjords: Kongsfjorden and Krossfjorden, Svalbard.

The Early Burst (EB) model emerged as the optimal fit for multivariate functional traits to offer critical insights into the evolutionary dynamics underlying Arctic macrobenthic diversification. This model implies an initial phase of rapid diversification followed by evolutionary deceleration (Harmon et al., 2010; Clavel et al., 2015). In Arctic fjords, the EB model may reflect rapid niche filling during postglacial colonization periods, when retreating ice sheets created extensive new benthic habitat and reduced interspecific competition (Stroeve et al., 2007; Wassmann et al., 2011). The subsequent evolutionary deceleration suggested by the EB model indicates that niche space became increasingly filled over time and limits opportunities for further adaptive diversification. These observed findings are in agreement with theoretical predictions for adaptive radiations in newly available habitat space, which was created by postglacial recolonization of Arctic fjords (Parkinson and Comiso, 2013; IPCC, 2021). The EB pattern observed in Arctic macrobenthos parallels findings from other marine adaptive radiations, including benthic-pelagic evolutionary transitions, where early burst dynamics were associated with colonization of novel ecological niches following mass extinction events (Harmon et al., 2010). Environmental position traits (Epi, In) fitted by EB models suggest that habitat utilization strategies underwent rapid early diversification followed by stabilization around optimal phenotypes. This pattern indicates epibenthic and infaunal lifestyles represent alternative adaptive peaks that were rapidly occupied during early Arctic colonization, with subsequent evolution constrained by the biomechanical and physiological requirements of each habitat strategy (Hansen, 1997; Cooper et al., 2016). The EB dynamics in environmental position traits may reflect the fundamental ecological trade-offs between surface-dwelling strategies that maximize feeding opportunities and burrowing strategies to provide protection from physical disturbance and predation (Belley and Snelgrove, 2016; Beauchard et al., 2017).

The fit of Brownian Motion (BM) models to univariate traits such as body size (Sm, Me, La) and motility (Mo, DM, Se) suggests more gradual and stochastic trait evolution within established phylogenetic lineages (Felsenstein, 1985; Blomberg and Garland, 2002). According to Puttick (2018), BM emerged as the most widely supported model for body size evolution for the majority of clades analyzed across mammals, birds, and squamates. According to this pattern, body size commonly evolves through neutral drift processes with variance proportional to evolutionary time, supporting BM as the appropriate evolutionary framework for univariate morphological traits. Moreover, Ferrón and Donoghue (2022) confirmed that BM outperformed other models in describing motility traits like swimming speeds in both early marine vertebrates and living fishes.

Feeding habit traits demonstrated heterogeneous evolutionary model support, with 'Car' and 'Sca' conforming to EB model, while 'SSDF', 'SDF', and 'SF' traits evolved under BM processes. Among living habitat traits, 'Tu', 'Bu', 'FS', and 'At' exhibited BM evolutionary patterns, except Cr, which followed EB trait evolution dynamics. This mixed evolutionary model pattern is supported by the work of Ingram et al. (2012), which shows that the EB model supports food webs with distinct trophic levels and limited omnivory. The EB dynamics in carnivorous and scavenging modes likely reflect discrete predatory niches with reduced overlap that promote early adaptive radiation. In contrast, Brownian Motion dynamics across most feeding and habitat traits suggest complex trophic interactions and extensive omnivory in marine ecosystems. These complex interactions refute Early Burst signals through continuous species turnover and recurrent trait evolution (Ingram et al., 2012).

The differential evolutionary patterns observed in our reproductive strategies (A, SS, and SB) may reflect varying selective pressures and adaptive constraints. Sol et al. (2025) used BM, OU, and multiple-optima OU models to explain various life history and reproductive trait evolution in marine endotherms. The results demonstrated that the reproductive traits followed slower evolutionary rates in marine as compared to terrestrial environments (Sol et al., 2025). Additionally, García-Rodríguez et al. (2023) used phylogenetic comparative methods (BM, EB, and OU) to analyse reproductive traits in Medusozoa and found that OU models provided the best fit for egg size evolution.

The comparative evolutionary models suggest that while overall trait diversification followed early burst dynamics, individual functional traits evolved more gradually within lineages. This finding highlights the complexity of evolutionary dynamics in Arctic systems, where different aspects of phenotype may respond to distinct selective pressures and evolutionary constraints (Harmon et al., 2010; Cooper et al., 2016). These evolutionary patterns are particularly relevant due to ongoing Atlantification and rapid Arctic climate change, which impose novel selective pressures that may exceed adaptive capacities of lineages

governed by deep phylogenetic constraints (Włodarska-Kowalczuk et al., 2012; Berge et al., 2016).

## 6. Conclusions

This study provides critical insights into the evolutionary dynamics in shaping functional trait variation in macrobenthic communities collected from 13 stations along the Arctic Kongsfjorden–Krossfjorden system, Svalbard. The integration of mtCOI phylogenies with a comprehensive functional trait database provides a robust framework to understand phylogenetic constraints that structure trait evolution in these fjords. The strong phylogenetic signal confirms evolutionary conservatism as a key driver in structuring functional traits of Arctic macrobenthos. Habitat traits like tube-dwelling and burrowing are especially conserved, reflecting adaptations to fjord conditions. Strong phylogenetic autocorrelation reveals deep evolutionary conservation of key functional traits in Arctic macrobenthos, supporting niche stability and adaptive resilience to environmental changes. A hierarchical pattern of evolutionary constraint reflects strong conservatism in living habitat traits, moderate in feeding habits, and high lability in reproductive strategies. The lecithotrophic larval mode in molluscs stands out as a specialized life-history adaptation that highlight evolutionary divergence within Arctic macrobenthic assemblages. Trait evolution followed different modes, with rapid early diversification in multivariate traits and gradual evolution of univariate traits like size and motility. These findings provide critical evidence that functional trait diversity in Arctic macrobenthos is deeply rooted in phylogenetic history. Simultaneously, the macrobenthic functional traits retain sufficient evolutionary flexibility to contend with rapid environmental change, including ongoing climate-driven Atlantification and glacial retreat. Understanding the evolutionary basis of trait variation is crucial for predicting the resilience and/or response of Arctic macrobenthic communities to rapid environmental changes. These findings underscore the importance of integrating phylogenetic frameworks with functional trait analyses for future Arctic macrobenthic monitoring studies. Hence, broad-scale evolutionary dynamics and ecological responses of macrobenthic communities under ongoing climate change are the need of the hour for guiding effective conservation and management strategies for these vulnerable fjord ecosystems.

## CRediT authorship contribution statement

**Snigdha Bhaumik:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Ahmed Shahir:** Writing – review & editing, Methodology, Formal analysis. **Sumit Mandal:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Sarat C. Tripathy:** Writing – review & editing.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107703.

## Data availability

Data will be made available on request.

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