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Contrasting biodiversity patterns across trophic levels in two Svalbard fjords: effects of Atlantic influence and physical isolation

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Contrasting biodiversity patterns across trophic levels in two Svalbard fjords: effects of Atlantic influence and physical isolation

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Abstract

Arctic glacial fjords are among the marine ecosystems most strongly affected by ongoing environmental change; however, comparative studies integrating responses across multiple ecological groups remain scarce. We present a multi-community biodiversity assessment of Kongsfjorden and Van Mijenfjorden, two Svalbard fjords with contrasting advective regimes. Kongsfjorden is an open fjord receiving significant warm Atlantic Water inflow whereas water exchange in Van Mijenfjorden is restricted by the island of Akseløya, resulting in longer water residence times and reduced Atlantic Water influence. Using datasets spanning three ecological groups − planktonic protists, zooplankton, and benthic macrofauna − we combined observational data with hydrodynamic modelling to explore how differences in advection affect taxonomic and functional diversity. Modelling revealed flushing times more than twice as long in Van Mijenfjorden as in Kongsfjorden (31. vs 13 days), supporting the hydrographic distinction of these systems. The contrasting hydrographic regimes were associated with biodiversity patterns that differed among the three ecological groups. Planktonic protist and zooplankton communities showed primarily seasonal differences between fjords, and were strongest during spring. Benthic macrofaunal communities showed a stronger fjord-level contrast than either planktonic group, and were differentiated primarily along the fjord axis, a pattern commonly associated with disturbance from glacial processes. Taxonomic and functional compositions were more strongly decoupled in pelagic than in benthic communities, potentially suggesting a greater functional redundancy within the plankton. The findings of this study demonstrate that biodiversity responses to contrasting hydrographic regimes differ among ecological groups and across spatial and temporal scales. Assessing ecosystem-wide effects of Atlantification requires coordinated, broadscale sampling across ecological components spanning seasonal, spatial and long-term temporal scales.

Keywords: Arctic; functional diversity; Atlantification; zooplankton; phytoplankton; benthos

1. Introduction

Rapid climate warming is occurring across the Arctic, leading to profound transformations of environmental conditions with cascading effects on marine ecosystems. The Svalbard archipelago is a hotspot of this warming, owing in part to its location directly adjacent to the major inflow of warm, saline and nutrient-rich Atlantic Water (AW) into the Arctic. Carried by the West Spitsbergen Current (WSC), these water masses move northward along the shelf of the western coast of Spitsbergen and are readily advected into the fjord systems, imparting a strong Atlantic influence on hydrography, nutrient regimes, and species composition. As a result, most of the western Spitsbergen fjords remain largely ice-free year-round and their biological communities host many Atlantic and boreal species (Hop et al. 2019c). The combined effects of oceanic heat transport that reduces sea-ice cover and enhances glacier melt (Luckman et al. 2015), and increased advection of boreal-temperate species – a process collectively termed "Atlantification" (Polyakov et al. 2020, 2025) – are likely to have complex and far-reaching consequences for ecosystem structure and functioning.

The extent to which this Atlantic impact manifests itself, however, varies considerably among fjords and depends strongly on the volume of AW advected into each system, which in turn is governed by fjord topography. Based on bathymetry and the presence and depth of sills, at least four fjord types can be distinguished in Svalbard: deep open fjords, semi-closed fjords, deep sill fjords, and shallow sill fjords (Søreide et al. 2021). All four types are found along Svalbard's western coast, lending themselves as natural laboratories to study the Atlantic impacts on ecosystems in the same bioregion. Sill fjords

with restricted exchange have been highlighted as particularly valuable systems for isolating community responses to local environmental conditions from advective signals (Renaud et al. 2007; Søreide et al. 2022). The strength of advective influence has been traditionally approximated by the ratio of mouth cross-sectional area to fjord volume (Aksnes et al. 1989; Basedow et al. 2004), although this may overlook the varying strengths of the currents between fjords, and therefore more sophisticated approaches use numerical model output to calculate the timescales of residence and flushing in a fjord using particle tracking (Torsvik et al. 2019; Lucas and Deleersnijder 2020). Two strongly contrasting systems in this respect are Kongsfjorden and Van Mijenfjorden.

Kongsfjorden is a deep open fjord in northwest Spitsbergen and is one of the best studied marine systems in the Arctic, hosting the world's longest Arctic observational time-series. This fjord lacks a sill, and KF is connected to the shelf slope through a deep glacial trough (Kongsfjordrenna, ~270 m) , leaving most of the water column open to exchange with warm, saline AW from the WSC (Tverberg et al. 2019). As a result, KF displays a strong and increasing Atlantic influence on its physical conditions, oceanography, and biological communities. Annual monitoring since 1996 has documented increasing temperatures and volumes of inflowing Atlantic Water (Tverberg et al. 2019; De Rovere et al. 2022), declining sea-ice (Pavlova et al. 2019), changes in seafloor community structure (Al-Habahbeh et al. 2020), changing phytoplankton bloom dynamics (Hegseth et al. 2019), and shifting proportions of Atlantic versus Arctic zooplankton species (Hop et al. 2019c). These changes have been propagating through the food web, with documented shifts in fish assemblages and seabird diets towards Atlantic prey (Vihtakari et al. 2018). Furthermore, the ongoing changes in fish communities are also expected to change the zooplankton communities through increased predation and competition from juvenile boreal species (Renaud et al. 2012).

Van Mijenfjorden, a shallow sill fjord located further south along the west coast, presents a starkly contrasting setting. Due to its peculiar topography with an elongated island (Akseløya) blocking almost its entire entrance, and water inflow restricted to two shallow sills, the direct connection with the WSC is limited and the amount of AW entering the fjord is strongly reduced. As a result, VMF experiences one of the most extensive and persistent sea-ice regimes remaining along the western Spitsbergen coast and constitutes one of the last sea-ice refuges in the west Svalbard region, providing a critical habitat for ice-dependent species such as ringed seals and polar bears (Bengtsson et al. 2021).

Numerous comparative studies have been conducted in Svalbard fjords, but they have typically focused on single ecological groups, such as prokaryotes (Costa et al. 2026), planktonic protists (Piwosz et al. 2009; Kubiszyn et al. 2014; Šupraha et al. 2022; Dragańska-Deja et al. 2024), zooplankton (Gluchowska et al. 2016; Ormańczyk et al. 2017; Weydmann-Zwolicka et al. 2021; Trudnowska et al. 2025), or benthos (Kędra et al. 2010; Włodarska-Kowalczuk et al. 2012; Górska and Włodarska-Kowalczuk 2017; Zaborska et al. 2018). Across pelagic communities, AW has been identified as a driver of interannual variability in phytoplankton bloom phenology (Hegseth and Tverberg 2013; Hegseth et al. 2019), prokaryote and protist taxonomic composition (Zhang et al. 2023; Costa et al. 2026), diatom abundances (Kubiszyn et al. 2014), and zooplankton community composition (Gluchowska et al. 2016). A higher diversity and a distinct composition of prokaryotes was reported for Kongsfjorden compared with the Arctic Rijpfjorden, linked to the higher nutrient uptake in the former (Costa et al. 2026). Comparing zooplankton communities in Hornsund, Isfjorden and Kongsfjorden during a warm period with extensive AW on the west Spitsbergen shelf (WWS). Similarly, Gluchowska et al. (Gluchowska et al. 2016) found that Isfjorden and Kongsfjorden contained higher proportions of boreal and cosmopolitan species, whereas the Arctic Water-influenced Hornsund was dominated by boreo-Arctic and Arctic taxa. Interannual contrasts in AW advection and sea-ice cover in Kongsfjorden have resulted in different taxonomic compositions of the phytoplankton spring-bloom communities, (Assmy et al.

2023), also reflected in strong interannual variability within the zooplankton (Hop et al. 2019c). Higher summer primary production was observed in the colder system of Hornsund compared to Kongsfjorden (Piwosz et al. 2009), whereas total zooplankton abundance and biomass were much higher in the latter (Ormańczyk et al. 2017). A biogeographic analysis of protist communities in five different Svalbard fjords, however, found the taxonomic diversity in Kongsfjorden and Van Mijenfjorden to be relatively similar, with a dominance of genotypes with an Arctic-temperate distribution, in contrast to Northern Svalbard fjords where more Arctic-endemic species were found (Šupraha et al. 2022). Similarly, Ormańczyk et al. (2017), did not find zooplankton species composition to differ substantially between Kongsfjorden and Hornsund in 2014.

In contrast to pelagic studies, comparative studies of benthic macrofauna across fjords of Spitsbergen have consistently documented strong glacially-driven disturbance as the dominant structuring factor. Włodarska-Kowalczuk et al. (2012) compared inner and outer basins of Kongsfjorden, Van Mijenfjorden and Hornsund to the open Barents Sea illustrating the unified response of a consistent pattern in fjord macrofauna taxonomic diversity. Species richness and diversity were generally lower in the innermost basins of fjords compared to the outer region or open shelf, and this pattern was associated with gradients in sedimentation and organic matter content rather than with water mass properties alone (Wlodarska-Kowalczuk et al. 2005). In Van Mijenfjorden, depth also had a strong structuring effect (Renaud et al. 2007) in addition to the location within the fjord. Similar relationships between glacier influence, disturbance and benthic community composition have also been documented not only in fjords of Spitsbergen (Renaud et al. 2007; Włodarska-Kowalczuk et al. 2012; Kędra et al. 2013), but also in Greenland (Sejr et al. 2010), Chile (Quiroga et al. 2022) and Antarctica (Pabis et al. 2015). These studies indicate that benthic macrofaunal community response to glacier disturbance rather than a phenomenon unique to Arctic fjords.

As species composition/taxonomic biodiversity alone does not provide direct information on the functional aspects of ecosystems and their changes, trait-based diversity analyses offer a complimentary approach. Traits are structural or functional characteristics of organisms that influence their performance and interactions with their environment (after (Violle et al. 2007; Dawson et al. 2021). As such, trait-based approaches allow to describe and compare different ecosystems with respect to their functional structure, and can also be used to relate aspects of diversity to community ecology and biogeochemical cycling (e.g., Litchman and Klausmeier 2008; Litchman et al. 2015). They are increasingly implemented in the analyses of Arctic marine ecosystems (Degen et al. 2018; Durazzano et al. 2025), with comprehensive trait databases becoming available for Arctic benthos (Degen et al. 2018;, zooplankton (Durazzano and Titocci 2026), and protists (Szeligowska et al. 2020), and several comparative studies previously conducted for Svalbard fjords (Włodarska-Kowalczuk et al. 2012, 2019; Trudnowska et al. 2025). In benthic macrofaunal communities of Svalbard fjords, distinct functional compositions have been observed in the fjord inner basins, where dominant traits likely represent adaptations to strong physical disturbance and low food availability (i.e., high mobility and detritivory) (Włodarska-Kowalczuk et al. 2012). For zooplankton, trait-based analysis of *Calanus* life-history characteristics distinguished Van Mijenfjorden as an "isolated" fjord type compared to all other fjords in West Spitsbergen, including Kongsfjorden (Trudnowska et al. 2025).

Despite growing interest in fjord ecology in the context of a changing Arctic, comparative multi-community biodiversity assessments remain limited (Descamps et al. 2026). Most studies address single ecological groups, single fjords, or single seasons, making it difficult to draw conclusions about how different trophic levels behave in Atlantic-influenced vs. partially-enclosed Arctic systems. Furthermore, only a few studies to date have integrated both taxonomic diversity and trait composition (Degen et al. 2018; Armitage et al. 2025; Gluchowska et al. 2025), and none comparing multiple

ecological groups simultaneously. Here, we synthesize published biodiversity data for planktonic protists, zooplankton, and benthic macrofauna from Kongsfjorden and Van Mijenfjorden, and translate taxonomic diversity data into functional diversity using a trait-based approach (Villéger et al. 2008). We combine these observational results with ocean modelling investigating residence time and exchange of water masses in these two fjords to quantify the difference in AW advection between the fjords. Specifically, we address the question to which extent the difference in AW advection between the open Kongsfjorden and Van Mijenfjorden affects taxonomic and functional diversity in these systems. We expect the imprint of Atlantic advection to differ among community types, and to vary seasonally and spatially depending on the timescales on which each community responds. Finally, by considering taxonomic and functional diversity together, we explore whether compositional differences between the fjords translate into differences in functional composition, or whether turnover among functionally similar taxa leaves the functional structure of these communities largely unchanged.

2. Methods

2.1 Study area

Kongsfjorden (KF) is a glacial fjord on the northwestern coast of Spitsbergen, Svalbard (78-79°N, 11-12°E), approximately 26 km long and 4-14 km wide, with maximum depths exceeding 300 m near the mouth. The fjord has no sill in its outer part and is directly connected to the shelf, allowing variable influxes of Atlantic Water; however, there is a 20 m deep sill separating the middle from the inner part. Van Mijenfjorden (VMF) is located further south on the western coast of Spitsbergen (77-78°N, 14-17°E), is approximately 83 km long, and separated from the relatively shallow and broad shelf by the narrow, elongated island of Akseløya, which creates a natural sill (Akselsundet, ~30 m depth) restricting water exchange. This feature helps maintaining colder and more stable water masses within VMF relative to the adjacent shelf, and delays ice break-up (Høyland 2009). Sampling stations in both fjords spanned along-fjord gradients from mouth to inner fjord, as well as a range of water depths (**Figure 1**).

2.2 Data sources and compilation

Published and publicly available datasets of planktonic protists, zooplankton, and benthic macrofauna spanning the study area were compiled from multiple sources spanning different sampling periods from 2007-2023 (**Table 1, Online Resource 1; Online Resource 7**). For simplicity, these three ecological groups will be referred to generally as phytoplankton, zooplankton, and benthos in figures. Original samples were collected with necessary permits from the competent authorities, if applicable, and the study is compliant with the Convention on Biological Diversity (CBD) and Nagoya protocols. Planktonic protist data were derived from water samples collected across multiple seasons and multiple stations/locations in both fjords between 2009 and 2022. From September 2015 to August 2016, integrated Remote Access Samplers (RAS–500, McLane) were deployed in KF and VMF enabling year-round autonomous collection of water samples for planktonic protist community composition and nutrient analyses (Smoła et al. in revision). Otherwise, sampling designs followed ongoing previous Svalbard time series deployments (Wallace et al. 2010; Hop et al. 2019a) and data are published (Cottier et al. 2021; Vogedes 2024). At sampling locations where multiple depths were sampled, planktonic protist abundances were averaged across depths. Zooplankton data were derived from vertical net hauls (Multinet or WP2, 180, 200 or 64 µm mesh size) conducted between March and October from multiple stations in KF during 2016-2023 (Assmy et al. 2023; Wold et al. 2024a, b) and VMF during 2016-2017 (Cuny 2017; Svendheim 2017), and 2022 (Trudnowska et al. 2026). Zooplankton samples were

processed under the stereomicroscope as described in (Cuny 2017; Svendheim 2017; Hop et al. 2019c). Abundances were converted to individuals m^{-3} for consistency across datasets and at sampling locations where multiple depths were sampled, abundances were depth-integrated. Multinet tows deeper than 200 m in KF were excluded to account for the much greater depth of this fjord; this was done in order to reduce the impact of deep-water taxa that would not be found in VMF due to its shallower depth rather than Atlantic connectivity. Developmental stage information was retained for *Calanus* spp. but integrated for all other species. Benthic macrofauna data were derived from grabs (van Veen and Petit Ponar) collected in both fjords covering mouth to inner fjord regions between 2007 and 2023 (Oleszczuk et al. 2021). After collection, grab contents were sieved (0.5 or 1 mm), preserved, and fauna were identified to the lowest taxonomic level possible. Abundances were converted to individuals m^{-2} for consistency across datasets and only samples collected deeper than 20 m were retained for analysis. Benthic primary producers, epifauna, and smaller size classes (meiofauna) were excluded from this data compilation, and data represents only the macrofaunal component of the benthic community.

Because the compiled datasets originated from independent studies, taxonomic resolution and nomenclature differed between sources. Taxonomy was therefore harmonised before analysis: nomenclature was adjusted according to WoRMS (WoRMS Editorial Board 2026), uncertain assignments (e.g., *sp. cf.*) were assigned to the corresponding binomial, synonyms were unified, spelling variants merged and infraspecific ranks were dropped. When possible, taxonomy was brought down to the lowest common denominator between sources (e.g., if one dataset identified a taxa only to genus level, those species were reduced to genus level across all datasets). Apart from one dataset each for planktonic protists and benthic macrofauna, individual data sources were restricted to a single fjord, so fjord identity and data source are partly confounded; this is addressed in discussion.

2.3 Environmental data and modelling

A high-resolution unstructured grid ocean model (FVCOM) (Chen et al. 2003) was run for the Svalbard west coast, covering both fjords under study and extending across the shelf into deeper water (**Figure 1**). This setup was described in (Herzke et al. 2021) and developed further in Ghaffari et al. (in prep.). Here, we extended the model with observed seasonal sea ice using the ICENUDGE model (Prakash et al. 2022) and run it for the period 2016-2017.

Bathymetry was based on the 50 m EMODnet bathymetry product (DTM 2024), with additional data from the Norwegian Mapping Authority. External forcing at the lateral boundaries was provided by the Met Norway Barents 2.5 km model (Röhrs et al. 2023) and forcing by the AROME-Arctic model output (Senter for utvikling av værvarslingstjenesten 2025). Observed ice cover which was extracted from high resolution remote sensing data retrieved from CMEMS (European Union-Copernicus Marine Service 2024). River data was provided from a mass balance model (van Pelt et al. 2019) and added as 1986 grid points along the coastline.

Lagrangian particle experiments to determine fjord flushing times were conducted with the particle tracking model PyLAG (Uncles et al. 2020). This was setup with a time splitting scheme using a 60 second RK4 advective timestep and an offset 30 second diffusion timestep using a constant horizontal diffusion (10 $m^2 s^{-1}$). Flushing times for the fjords were calculated by releasing one million particles for each month uniformly distributed in the fjord area (**Figure 1)** and then counting the percentage remaining at each step, with the flushing time defined as when only 1/e (~37%) remain within the fjord area (Monsen et al. 2002). The flushing time is a bulk property of a water body which defines the timescale for exchange of the water with its surroundings. Its approximation by the e-folding time (when

1/e particles remain) is by analogy to an idealised model of a continuously stirred water body, where the time to reach 1/e represents the average amount of time the substance stays in the system.

Hydrographic data from CTD casts were obtained from the UNIS CTD archive (Berge et al. 2024), the the NPI's annual (Marnela et al. 2024) and seasonal pelagic monitoring in Kongsfjorden (Bailey et al. 2026) and other available CTD data. Planktonic data were matched to the closest available CTD cast in space and time, with accepted matches not exceeding 7 days and/or 10 km away. CTD data matching these criteria was found for 385 of 410 planktonic samples (94%). For each matched cast, mean temperature and salinity were calculated for the surface (upper 10 m) and bottom (lower 10 m) layers and for the entire water column, and a stratification index was calculated as the difference in density between 1 m and 50 m (or the deepest measurement at shallower stations). For planktonic protist samples collected with the remote access sampler (RAS), only upper water column measurements were available. Since benthic macrofaunal communities are composed of long-lived taxa that integrate environmental conditions over years, hydrographic conditions on the day of sampling are less informative than the overall regime at each station. Thus, instead of concurrent CTD data, we extracted station-level environmental variables from modelled hydrographic profiles that covered a full annual cycle from 1/5/2016 to 31/4/2017. Parameters extracted included mean and minimum bottom temperature, minimum bottom salinity, proportion of the year classified as Atlantic-derived water and mean annual stratification index. Water masses were assigned based on temperature and salinity values using definitions in, both for observed and modelled temperature-salinity data.

2.4 Taxonomic and functional diversity analyses

Preliminary analyses were performed to assess broad patterns in community structure and identify relevant environmental groupings for subsequent analyses (**Online Resource 2**). Based on these exploratory analyses, planktonic protist and zooplankton samples were assigned to three seasonal periods representing major phenological transitions (March-May, June-July, August-October), whereas benthic macrofauna samples were assigned to three categories representing distinct fjord basins (Shelf, Outer, Inner, **Figure 1**). These groupings were retained for all subsequent taxonomic and functional community analyses. All analyses were done in R v. 4.4 (R Core Team 2024).

The traditional alpha diversity metrics -- species richness (S), Pielou's evenness (J'), and Shannon diversity (H'), which integrates the previous two metrics -- describe how many taxa are present per sample and how evenly abundance is distributed among them, treating all species/taxa as equally distinct. These metrics were calculated at the station level for all ecological groups using the package *vegan* (Oksanen et al. 2026). Differences in taxonomic diversity between fjords were assessed separately for each ecological group using Wilcoxon rank-sum tests with Benjamini-Hochberg corrections for multiple comparisons. Planktonic protist and zooplankton metrics were compared across fjords within seasons (March-May, June-July, August-October) while benthic macrofauna diversity metrics were compared across fjords within distinct basins (inner, outer, shelf). Species richness was not pooled by fjord for comparison, so the unequal number of samples between fjords does not drive results of these analyses.

Functional trait information was assigned to species using trait databases compiled from published sources (Willis et al. 2006; Degen and Faulwetter 2019; Gluchowska et al. 2025; Durazzano and Titocci 2026) and expert assessment if no published trait information was available at the time of analysis. Planktonic protist traits included environment of origin (ice, water), group (ciliates, centric diatoms, pennate diatoms, dinoflagellates, flagellates, other), life form (chain/colony, single cell), size (up to 20 µm: nano; larger than 20 µm: micro), and predominant trophic mode (phototroph, heterotroph,

mixotroph). For zooplankton, traits included body size, biogeographic affinity (Arctic, boreo-Arctic, boreal, Atlantic, cosmopolitan), depth habitat (cryopelagic, neritic, oceanic, shelf), feeding mode (cruise, active ambush, passive ambush, current), diet (carnivore, herbivore, omnivore, parasite), transparency (gelatinous, non-gelatinous), spawning strategy (egg carrier vs. free spawner) and depth (epipelagic, mesopelagic, bathypelagic, hyperbenthic). For benthic macrofauna, traits included biogeographic affinity (Arctic, boreo-Arctic, boreal, cosmopolitan), larval development type (lecithotrophic, planktotrophic, direct), lifespan (> 20 years, 5-20 years, 2-5 years, < 2 years), movement type (swimmer, crawler, burrower, sessile) and body size (> 300 mm, 100-300 mm, 50-100 mm, 10-50 mm, < 10 mm). Traits were fuzzy coded: each trait was divided into modalities, and every taxon was assigned an affinity to each modality and scaled between 0 and 1 with a sum of 1 across all modalities within a trait (e.g. a taxon recorded as "epi/mesopelagic" received 0.5 for each of the two depth modalities, and one recorded across three size classes 1/3 for each). When trait information was not available for a taxon, all modalities of the missing traits were set to 0 rather than to NA, which allowed to keep these taxa in the analysis without them contributing affinity to the missing traits. For all groups, three functional diversity metrics (Magneville et al. 2024) were calculated at the station level using the mFD package in R: functional richness (FRic), functional evenness (FEve), and functional dispersion (FDis). These are analogous to the three traditional taxonomic diversity metrics (S, J', H') but weigh species on their functional role in the community: FRic measures the total volume of trait space occupied, FEve describes how evenly the abundance is distributed across the trait space, and FDis quantifies the spread of taxa around the community trait centroid, and thus the degree of functional differentiation among dominant taxa (Laliberté and Legendre 2010; Magneville et al. 2024). Differences in functional diversity between fjords were assessed using Wilcoxon rank-sum tests comparing Fric, FEve and FDis of each group. Planktonic protist and zooplankton metrics were compared across seasons, and benthic macrofauna metrics were compared across fjord basins. For each combination of ecological group and season/fjord basin, differences between fjords were tested independently, and resulting *p*-values were adjusted for multiple comparisons within each diversity metric using the Benjamini-Hochberg procedure to control the false discovery rate.

Indicator species analysis (IndVal) (Dufrêne and Legendre 1997) was used to identify taxa significantly associated with either fjord. For each ecological group, the group-equalized indicator value index, which corrects for unequal numbers of samples between groups, was calculated using the *indicspecies* package (Cáceres et al. 2025). This index combines a specificity component (A, the probability that a sample belongs to the given fjord when the taxon is present) and a fidelity component (B, the probability of finding the taxon in samples from that fjord). Statistical significance of the resulting values was assessed with permutation tests (999 permutations), and p-values were adjusted using the Benjamini-Hochberg correction, consistent with the univariate diversity comparisons.

Taxonomic community composition was assessed using Bray-Curtis dissimilarities calculated from Hallinger-transformed abundances followed by Principal Coordinates Analysis (PCoA). A Hellinger transformation was chosen to highlight patterns based on relative composition, rather than raw abundance or species richness, and to reduce the influence of highly abundant taxa and right-skewedness while retaining among-sample differences. PCoA orders axes by the total variance they explain and are conventionally visualized using the first two PCoA axes which explained the greatest percentages of variation. For zooplankton, we show Axes 1 and 3, as Axis 3 carried the fjord contrast, while the conventional PCoA1/PCoA2 ordination is given in **Online Resource 6**. All other ordinations show axes 1 and 2. The separation of fjord and season/basin centroids and taxa significantly associated with the ordination were identified using *envfit* ($p < 0.05$) and were displayed as biplots, where the vector direction indicated the direction of association with the ordination axes and vector length reflected the strength (R^2) of the association.

Functional composition was explored by calculating Community Weighted Means (CWMs) of abundance-weighted fuzzy coded trait matrices using the FD package in R (Laliberté and Legendre 2010). Trait modalities were weighted equally within each trait category to ensure equal contributions to distance measures, regardless of the number of modalities present per trait. Gower distance was used to calculate dissimilarities among samples of CWMs and if the resulting distance matrix was non-Euclidean, a Cailliez correction was applied prior to conducting PCoA. Ordinations were visualized using the first two PCoA axes. Traits that were significantly associated with these ordination axes were displayed as vectors which point in the direction of the association with a length that is scaled to the strength of the association. Ellipses in ordination plots represent 95% confidence ellipses for data grouped by fjord.

Permutational multivariate ANOVA (PERMANOVA, 999 permutations) (Anderson 2001) was used to test for significant differences in community and functional composition between fjords, seasons (planktonic protists and zooplankton) or fjord basins (benthic macrofauna) using the package vegan (Oksanen et al. 2026) on Bray-Curtis and Gower dissimilarity matrices, respectively. Since PERMANOVA is sensitive to heterogeneity of multivariate dispersion, each factor was examined for homogeneity with permutation tests (Anderson 2006). For benthic macrofauna, replicates were averaged within each station/sampling date prior to analysis to avoid pseudoreplication. Shelf stations were excluded from the benthic PERMANOVA as they were represented by too few samples, precluding a balanced test of the fjord × basin interaction; the analysis therefore compared only the outer and inner basins of the two fjords. The correlation between taxonomic and functional dissimilarity structures was calculated for each community type using Mantel tests on the two distance matrices (Spearman rank correlation, 999 permutations). Because community-weighted trait values are derived from the same abundance data, some level of congruence between them is expected by design, and the informative value of the correlation lies not its absolute value, but how its magnitude varies among the ecological groups.

2.5 Environmental drivers of community composition.

Examined environmental parameters included CTD-derived temperature, salinity, stratification index, bottom depth, and proportion of the year classified as Atlantic-derived water. For planktonic protists and zooplankton, surface values of temperature and salinity were used while for benthic macrofauna the mean and minima of these parameters were used as they are more meaningful for long-lived and primarily sedentary organisms. Relationships between these parameters and the unconstrained ordinations were first examined by fitting environmental vectors onto the taxonomic and trait-based PCoA ordinations using envfit in vegan (999 permutations), with significance established at $p < 0.05$. The amount of compositional variation attributable to the measured environmental variables was quantified using distance-based redundancy analysis (dbRDA) (Legendre and Anderson 1999), applied to the same Bray-Curtis (taxonomic) and Gower (trait) distance matrices used for the PERMANOVA. The significance of the overall model and of individual terms was assessed by permutation tests (999 permutations), and model fit was expressed as adjusted R^2.

To separate the contributions of hydrography, fjord identity, and season/fjord basin, we performed variation partitioning, which decomposes the explained variation into unique and shared fractions attributable to each set of explanatory variables (Borcard et al. 1992; Peres-Neto et al. 2006). Fractions are reported as adjusted R^2; negative values, which can arise when a fraction explains no more variation than expected by chance, are interpreted as zero. Since the fjords differ systematically in hydrography, and hydrography also varies seasonally, a substantial proportion of the explained variation is expected to be shared among the three sets.

3. Results

3.1 Physical characteristics

The ocean model showed that the two fjords differed in their physical characteristics. The restricting impact of Akseløya and the the shallow sill at the entrance to Van Mijenfjorden (VMF) was visible in the mean summer surface temperature (**Figure 3**). In Kongsfjorden (KF), temperatures were relative uniform within the entire fjord (~4-5 °C, with a difference of less than ~1 °C between the fjord mouth and the inner basin), whereas in VMF temperature showed a pronounced change from ~4.5-5 °C on the shelf west of Akseløya to below 3 °C inside VMF. Water inside VMF was therefore approximately 1.5-2°C cooler than water of the same latitude outside Akseløya.

The difference was even more pronounced in the distribution of water masses along each fjord (**Figure 4**). The seasonal cycle in water masses demonstrated that both fjords contained Atlantic Water at their western boundary, which mixes with colder shelf water in winter to form Transformed Atlantic Water (TAW). In KF, AW/TAW extended along the entire fjord below the Surface Water (SW) whereas in VMF no water masses beyond Akseløya were classified as AW/TAW. The AW/TAW signal in KF was also weaker in the small inner basin behind the inner sill, which was instead occupied by Local Water (LW) in spring and winter and by Intermediate Water (IW) in summer and autumn. Intermediate Water (IW) occupied a large proportion in both fjord basins and is defined, defined as the product of mixing of AW and SW (Cottier et al. 2005). The reduced intrusion of warm AW into VMF, combined with its considerably shallower basin (<140 m, compared with >300 m in KF), contributed to the inner fjord being dominated year-round by locally formed water masses: colder fresher water in a comparatively thick layer at the surface (LWF, WCWF, SW) with LW underneath in spring and winter, and IW in summer and autumn.

Reduced circulation was also reflected in the mean flushing time, which was considerably longer for VMF (31.4 days) compared to KF (13 days). VMF flushing times exceeded those of KF in every month except May, but with considerable seasonal variation in both fjords (**Figure 5**). Both showed a spring maximum (53 days in VMF in April and 38 days in KF in May) likely due to the onset of spring stratification. Outside this period, KF flushing time was stable at 11-13 days, with lowest values observed in February (6 days) and November (7 days), while VMF ranged from 19 days in November to ~35 days through mid-winter and summer, i.e. roughly 2-3 times longer than KF for most of the year. VMF is longer and shallower than KF, with a volume ratio of 1.4 (33.27 km^3 compared to 23.23 km^3 for the volume used for the flushing time calculation), which accounts for some of this difference; however, it still implies more restricted circulation between the fjord and shelf in VMF.

In terms of the volumes used to calculate flushing time, the cross-sectional area across which exchange takes place was much smaller in VMF (40.6 x 10^3 m^2) compared to KF (1971.8 x 10^3 m^2), however this constriction also led to much stronger tidal currents at the VMF entrance (mean peak surface tidal current 1.88 ms^{-1}) compared to KF (0.31 ms^{-1}). This resulted in similar gross transport in both, despite the area difference, but in VMF much of this water was cycled back and forth within a tidal cycle resulting in residual transport into VMF still being an order of magnitude lower than KF (**Online Resource 4**). The opening to VMF is also relatively shallow (44m at its deepest point), so the water exchange was occurring primarily from IW outside the fjord and not the deeper AW as in KF.

3.2 Taxonomic diversity

Differences in sample-level (alpha) diversity between fjords were observed in all 3 community types during certain seasons (plankton) or fjord basins (benthos), although typically they did not extend to all three metrics (**Figure 5, Online Resource 4**).

Planktonic protists displayed the highest absolute per-sample species richness (S) of the three ecological groups, with values up to 75 species per sample, and showed a pronounced seasonal shift in VMF (lowest in spring, highest in autumn, $p < 0.05$), but not in KF. Shannon diversity (H') rose significantly ($p < 0.05$) from spring to autumn in both fjords, and evenness (J') only in KF. During spring, species richness was significantly higher in KF than VMF ($p_{adj} = 0.018$); during summer and autumn this trend was reversed, but these differences were not statistically significant. No significant differences between fjords were detected for H' or evenness J' during any season.

Zooplankton showed more fjord-level differences in alpha diversity that the other groups (**Figure 5**), mostly driven by pronounced seasonal shifts in all three metrics in VMF, while in KF they remained relatively constant. As a result, richness (S) was significantly higher in KF during spring ($p_{adj} = 0.005$), but this pattern did not persist into summer or autumn. On the other hand, H' and J' were significantly higher in KF during June-July ($p_{adj} = 0.018$ and 0.015, respectively). The differences in H' and J' during other times of year were not pronounced, although J' trended higher in VMF during spring ($p = 0.07$).

Taxonomic diversity of benthic macrofauna varied by fjord basin in both fjords and was significantly different between KF and VMF in different parts of the fjord systems (**Figure 5**). Species richness (S) and Shannon diversity (H') generally decreased from the outer basin to the inner basins of the fjords. Evenness (J') of the communities showed greater variability inside the fjord than on the open shelf. In the outer basin stations, H' and J' were both significantly higher in VMF than in KF (H': $p_{adj} = 0.014$; J': $p_{adj} = 0.002$) while S was similar, suggesting that while total species per sample were not significantly different, the outer VMF community was characterized by a more even distribution of abundances across taxa. No significant differences between fiords were detected at the inner basin stations for any diversity metric, although the variability in both S and H' in KF was much higher than in VMF.

Indicator species analysis did not identify any taxa exclusively associated with one of the fjords, although several taxa in all three ecological groups showed a significant level of preferential affinity for either KF or VMF (**Online Resource 5**). For planktonic protists, associations were the weakest of the three ecological groups (indicator values ≤ 0.65): the strongest KF "indicator" was the choanoflagellate *Calliacantha natans* (IndVal = 0.65), whereas the few VMF-associated taxa included athecate dinoflagellates (*Gymnodinium* and *Gyrodinium* spp.) and pennate diatoms (*Amphiprora kjellmanii, Pleurosigma stuxbergii)*. Zooplankton "indicators" were strongly skewed towards VMF, and included neritic copepods (*Acartia* spp., *Microsetella norvegica*) and meroplanktonic larvae, while only the euphausiids *Thysanoessa inermis and T. longicaudata* and the copepod *Paraeuchaeta* spp. were identified as significantly associated with KF. The benthos showed the opposite pattern, with most indicators associated with KF (including *Nephtys ciliata*, *Yoldiella lenticula* and others), while VMF was characterized by few but very strongly associated taxa, most notably polychaetes *Polycirrus arcticus* and *Aglaophamus malmgreni* (indicator values > 0.9).

3.3 Functional diversity and trait composition

Functional diversity of planktonic protists was largely similar between the two fjords during all seasons (**Figure 6, Online Resource 4**), although several metrics exhibited different seasonal patterns within each fjord. Functional diversity (FRic) declined significantly from spring to summer/autumn in KF but not in VMF. Functional dispersion (FDis) followed a similar pattern in KF, decreasing stepwise from

spring to summer and from summer to autumn, while in VMF only the summer –to autumn decline was significant ($p_{adj} < 0.05$). Neither FRic nor FDis differed significantly between KF and VMF in any season. The only significant contrast between fjords was observed for functional dispersion (FEve), which was higher in KF during autumn ($p_{adj} < 0.05$). Averaged across seasons, the mean trait composition showed some differences between the fjords (**Figure 7a**). Although primarily pelagic taxa dominated the protist communities in both fjords, VMF communities contained roughly double the proportion of primarily ice-associated taxa. The KF communities contained a higher proportion of flagellates, mixotrophic taxa and nano-sized plankton, whereas the VMF community was characterized by greater proportions of diatoms, phototrophic taxa and cells larger than 20 µm.

Zooplankton showed significant differences between fjords in functional richness (FRic) ($p_{adj} < 0.001$) and functional dispersion (FDis) ($p_{adj} = 0.021$), but only during spring (**Figure 6**). These differences disappeared in summer and autumn, when the VMF and KF metrics converged. This seasonal pattern was driven primarily by changes in VMF, where FRic increased significantly from a near-zero minimum in March-May, while in KF it did not vary significantly across the season. FEve declined significantly from spring to later seasons in both fjords but did not differ between fjords in any season. FDis showed the most pronounced seasonal trajectory in both fjords, decreasing significantly in June-July before recovering by August-October to similar levels as in spring. Mean composition also differed between the fjords for several traits (**Figure 7b**). The zooplankton communities in KF were characterized by a higher proportion of carnivores, larger individuals and oceanic species, while VMF was dominated by smaller, neritic, and omnivorous species. The KF community also contained a higher relative proportion of Atlantic taxa, while VMF was characterized by a higher relative contribution of boreo-Arctic and cosmopolitan species. Notably, the contribution of true Arctic species was comparable between the fjords.

Benthic functional diversity showed clear gradients along the fjord axis that differed between fjords and among metrics. Only functional evenness within the outer basin was significantly higher in VMF than in KF (FEve: $p_{adj} <0.05$). Functional richness showed a clear increasing trend from inner to outer VMF, whereas no trend was found in KF. Conversely, FEve and FDis increased down-fjord in KF but not in VMF. As observed in taxonomic diversity metrics, the variability of functional diversity metrics was the highest in the inner fjord for both KF and VMF and no metric differed significantly between fjords for the inner basins.

The benthic macrofauna communities in KF and VMF also exhibited modest differences in trait compositions (**Figure 8c**). A greater proportion of taxa with direct development or lecithotrophic larvae, medium to long life spans (5-20 and >20 years), and large body sizes (>300 mm) were present in VMF compared to KF (**Figure 8c**). Interestingly, there was no clear indication that the VMF community had a greater proportion of Arctic species as would have been expected given the environmental conditions in contrast to KF. Instead, VMF contained a slightly greater proportion of cosmopolitan species and a lower proportion of Arcto-boreal species than KF. Movement modes represented in the communities were similar in the two fjords with a very slightly lower proportion of sessile macrofauna in VMF compared to KF.

3.4 Taxonomic and functional community structure and environmental drivers

3.4.1 Planktonic protists

Taxonomic composition and/or dispersion of planktonic protist communities differed significantly but weakly between fjords (PERMANOVA: $p = 0.001$, R^2=0.04) and more strongly among seasons ($p = 0.001$, R^2=0.11), with a significant fjord × season interaction ($p = 0.020$, $R^2 = 0.02$) (**Online Resource 6**). Multivariate dispersion was homogenous among seasons ($p = 0.11$) but differed significantly between fjords ($p < 0.001$), with VMF samples exhibiting greater among-sample heterogeneity, and making the fjord PERMANOVA contrast inconclusive. The first two PCoA axes captured 27.0% of the variation, with the first axis (16.4%) dominated by a seasonal signal and a fjord separation visible in the second axis (10.6%) (**Figure 8a**, left). The fjord centroids were significantly separated on the ordination ($p = 0.001$, R^2=0.08), but with extensive overlap between their 95% ellipses. Hydrographic variables were also significantly correlated with the ordination ($p = 0.001$); surface salinity ($R^2 = 0.43$) and stratification index ($R^2 = 0.39$) roughly aligned with Axis 1, pointing towards opposite ends of the ordination space, while the surface temperature vector ($R^2 = 0.48$) pointed towards the quadrant occupied by summer and autumn KF stations, associated with small flagellates, *Phaeocystis pouchetii*, cryptophytes (*Cryptomonas* spp.) and athecate dinoflagellates. The opposite (lower-right) quadrant was mostly occupied by springtime VMF stations and a few spring KF stations and was associated with elevated abundances of diatoms, some associated with sea ice (*Fragilariopsis cylindrus*, *F. oceanica* and *Navicula* spp). This area of the ordination also held the water mass centroids for ArW and WCW, while the Atlantic-derived and intermediate water centroids (AW, IW, TAW) sat on the KF side of Axis 2 and the freshwater-influenced local water centroid (LWF) fell within the VMF cluster. The dbRDA constrained on hydrography alone explained just 15.1% of taxonomic composition variation ($R^2_{adj} = 0.136$), with marginal significance in surface temperature ($p = 0.001$), surface salinity ($p = 0.002$) and stratification ($p = 0.006$). Variation partitioning attributed little of the explained variation uniquely to any single component, although each set accounted for an appreciable amount when fitted alone (**Online Resource 6**). Of total 23.0% explained variation, 9.3% of variation was attributable uniquely to any one set (Season – 5.0%; Fjord – 2.3%), with 77.0% unexplained (**Online Resource 6**).

Trait composition of planktonic protists showed a comparably weak but significant difference between fjords (PERMANOVA: $p = 0.001$, $R^2 = 0.05$), whereas seasonal variation was much stronger ($p = 0.001$, $R^2 = 0.24$), with a significant interaction ($p = 0.001$, $R^2 = 0.02$) (**Online Resource 6**). Compared with taxonomic composition, the proportion of variation explained by fjord identity was lower, while that attributable to season was more than twice as high, suggesting that trait composition was governed primarily by seasonal succession. Multivariate dispersion differed significantly between fjords ($p = 0.001$), with VMF samples more dispersed than KF samples, and among seasons ($p = 0.017$), decreasing progressively from spring to autumn. The trait ordination was considerably more structured than the taxonomic one, with the first two axes capturing 61.8% of variability. Axis 1 (41.6%) described a gradient from single-celled, mixotrophic and heterotrophic flagellate-dominated communities towards chain- or colony-forming, phototrophic, diatom-dominated communities (**Figure 8a**, right). The separation between fjords, however, was weak ($p = 0.001$, $R^2 = 0.05$, $p < 0.001$) with almost full overlap, although VMF stations extended further towards the diatom end of Axis 1 and the KF ellipse was displaced towards the flagellate end. Hydrographic vectors mapped directly onto this gradient: surface temperature ($R^2 = 0.50$) and stratification index ($R^2 = 0.41$) both pointed into the upper-left quadrant occupied by summer and autumn KF stations and by the single-celled, heterotrophic and dinoflagellate trait vectors, while surface salinity ($R^2 = 0.38$) pointed towards the opposite, lower-right quadrant holding the chain/colony, phototroph and ice-habitat vectors (all $p = 0.001$). The ArW and WCW centroids again fell on the diatom side of the ordination and the AW and IW centroids on the flagellate side. The dbRDA explained 31.0% of trait composition variation ($R^2_{adj} = 0.289$), but only surface temperature ($p = 0.002$) and bottom temperature ($p = 0.028$) were significant in the marginal tests.

Variation partitioning similarly attributed little unique variance to any single variable, with the most explained variance shared between temperature, salinity and season and 60.0% unexplained (**Online Resource 6**).

3.4.2 Zooplankton

Zooplankton taxonomic composition also differed significantly between fjords (PERMANOVA: $p = 0.001$, R^2=0.09), and seasons ($p = 0.001$, $R^2 = 0.18$), with a significant fjord × season interaction ($p = 0.001$, $R^2 = 0.05$) (**Online Resource 6**). Together, these explained 32% of the total variation. Multivariate dispersion did not differ between fjords ($p = 0.60$) but varied strongly among seasons, decreasing from spring to autumn: spring communities were compositionally more heterogenous and converged as the season progressed. The first two axis of the PCoA explained 40.4% of the variation in zooplankton taxonomic composition, with both axes reflecting seasonal patterns. The third axis (9.4% variance) carried the contrast between fjords; Axes 1 and 3 are therefore shown here (35.9% of the variation; **Figure 8b**, left). PCoA displayed with traditional axes 1 and 2 are shown in **Online Resource 6**. Spring and early-summer VMF stations were clustered in the upper part of the ordination, associated with *Microcalanus* spp., *Microsetella norvegica*, *Acartia* spp., and *Calanus glacialis.* Late summer stations from both fjordsoccupied the lower part of the ordinatiom, associated with *Oithona similis*, *O. atlantica*, *C. finmarchicus*, *C. hyperboreus*, *Limacina helicina* and *Themisto abyssorum*.

In contrast to the protists communities, the hydrographic vectors were aligned primarily with the fjord-related axis rather than the seasonal gradient. Surface temperature ($R^2 = 0.44$) and stratification index ($R^2 = 0.32$) pointed almost directly downwards into the KF cluster also containing the centroids for AW/TAW, while surface salinity ($R^2 = 0.33$) pointed in the opposite direction, into the VMF cluster and WCW/ArW. The dbRDA explained 19.7% of variation (R^2adj = 0.167). All five hydrographic variables were significant in the marginal tests and surface temperature the strongest ($p = 0.002$). Variation partitioning was significantly less confounded than for the protists, and gave season by far the largest unique fraction (13.0%), ahead of temperature and salinity combined (7.5%) and fjord identity (5.2%), with stratification contributing almost nothing independently (0.1%) and 58.9% unexplained (**Online Resource 6**).

Trait composition of zooplankton showed a similar pattern observed for taxonomic composition, with significant separation between fjords (PERMANOVA: $p = 0.001$, $R^2 = 0.09$) and a slightly weaker seasonal signal ($p = 0.001$, $R^2 = 0.17$), with a significant fjord × season interaction ($p = 0.001$, $R^2 = 0.04$) (**Online Resource 6**). Multivariate dispersion was homogenous between fjords ($p = 0.44$) but differed significantly among seasons ($p = 0.001$), being highest in spring, lowest in June-July and intermediate again in autumn, rather than declining progressively as was observed in the zooplankton taxonomic composition. The first two axes captured 52.4% of the variability (**Figure 8b**, right), with the fjord separation was carried by Axis 2 (15.7). Axis 1 (36.7%) was primarily shaped by season and showed a gradient from communities of large, free-spawning, current-feeding Atlantic and Arctic calanoids in June-July towards communities of small (XS), egg-carrying, active ambush-feeding, boreo-Arctic and cosmopolitan copepods in spring and autumn. Axis 2 separated large, gelatinous, carnivorous and mesopelagic taxa on the KF side from small, non-gelatinous, neritic and egg-carrying taxa on the VMF side. Fjord centroids were significantly but weakly separated ($p = 0.001$, $R^2 = 0.08$), the VMF cluster being displaced towards the lower-right of the ordination with extensive overlap between the 95% ellipses. Hydrographic vectors were weaker here than in any other ordination and were oriented along the fjord axis: the stratification index ($R^2 = 0.14$) pointed downwards into the VMF quadrant, while surface salinity ($R^2 = 0.19$) pointed in the opposite direction, towards the large,

gelatinous and carnivorous vectors on the KF side (both $p = 0.001$). Surface and bottom temperature were not significantly correlated with the trait ordination ($R^2 = 0.03$, $p = 0.15$) and are not shown. The dbRDA explained 14.4% of trait composition variation ($R^2_{adj} = 0.113$), and variation partitioning gave season the largest unique fraction of any response in the study (15.4% of the total 24.0% it explained alone), with fjord identity (4.8%) and hydrography (4.7%) essentially tied behind it and stratification negligible (0.2%), leaving 63.3% unexplained (**Online Resource 6**).

3.4.3 Benthic macrofauna

Benthic macrofaunal communities showed the highest contrast between fjords among the three studied ecological groups (PERMANOVA, $p = 0.001$, $R^2 = 0.14$), with significant differences between the outer and inner basins ($p = 0.001$, $R^2 = 0.11$), and a significant fjord × basin interaction ($p = 0.002$, $R^2 = 0.07$); together these terms explained 32% of the compositional variation (**Online Resource 6**). Multivariate dispersion was homogeneous between fjords ($p = 0.80$) but differed significantly between basins ($p = 0.001$), with inner-basin communities being more dispersed than outer-basin communities. On the PCoA ordination, a strong spatial gradient was observed in the community composition of benthic macrofauna within VMF (**Figure 8b**, left), where the stations separated into 3 distinct groups based on their position in the fjord. In KF the gradient was shaped by depth rather than fjord basin, with the shallow stations forming a distinct group, while the deeper KF stations clustered with the VMF shelf stations. There was a significant separation between fjords overall ($p = 0.001$, $R^2 = 0.23$), and the ordination was significantly correlated with water depth ($R^2 = 0.52$), the duration of Atlantic Water influence ($R^2 = 0.49$) – both of which pointed towards the deep KF cluster – and mean bottom temperature ($R^2 = 0.54$), which was inversely correlated with the inner VMF group. The VMF grouping was associated with the abundance of three species: the polychaetes *Aglaophamus malmgreni* and *Polycirrus arcticus* and the bivalve *Portlandia arctica*, mirroring the indicator-species analysis. The shallow KF stations were associated with higher contributions of *Cossura longocirrata*, *Chaetozone* spp. and *Eteone* spp., while the deep stations were separated via polychaetes such as *Lumbrineris* spp., *Maldane sarsi*, *Galathowenia oculata*, *Myriochele heeri, Heteromastus filiformis* and others. The dbRDA explained 44.3% of variation ($R^2_{adj} = 0.308$). In the marginal tests, fjord basin ($p = 0.001$), mean bottom temperature ($p = 0.003$) and depth depth ($p = 0.004$) were significant, with neither salinity, water-mass residence nor stratification significant once the others were accounted for. Given that depth, salinity and Atlantic Water residence are collinear in this system ($r = 0.81$ for AW duration for both depth and salinity), these tests are thus better interpreted as identifying a single gradient than as ranking independent drivers. Variation partitioning separated explanatory variables into four sets. Station position (depth and basin combined) was both the largest overall contributor (adjusted $R^2 = 0.233$, when fitted alone) and the least redundant, retaining 0.138 uniquely once the other sets were accounted for. Fjord identity contributed less overall (0.117) but about half of that independently (0.057), whereas hydrography and water-mass residence were largely redundant with the other sets, retaining only 0.031 and 0.012 of their respective 0.163 and 0.136. Summed, the fractions accounted for total 37.0% explained variation and 63.0% unexplained. Benthic species turnover was therefore structured principally by where a station sits within the fjord system (**Online Resource 6**).

Benthic trait composition mirrored the taxonomic composition, differing significantly between fjords (PERMANOVA, $p = 0.001$, $R^2 = 0.15$) and basins ($p = 0.001$, $R^2 = 0.14$), with a significant fjord × basin interaction ($p = 0.001$, $R^2 = 0.06$). The ordination showed a significant, but slightly less pronounced separation between fjords ($p = 0.001$, $R^2 = 0.18$), with significant overlap between them (**Figure 8c,** right) and a stronger separation by basin ($p = 0.001$, $R^2 = 0.30$). Depth was by far the strongest environmental correlate of any variable in any ecological group ($R^2 = 0.70$) and pointed directly along Axis 1 into the KF cluster, with the duration of Atlantic Water influence ($R^2 = 0.52$) and

mean bottom temperature ($R^2 = 0.46$) close beside it. The dbRDA of benthic trait composition explained 45.0% of variation ($p = 0.001$, $R^2_{adj} = 0.313$). Only mean bottom temperature ($p = 0.015$) and depth ($p = 0.038$) were significant in the marginal tests; basin, stratification, salinity and water-mass residence were not significant. For variation partitioning of trait composition, the same four sets explained a comparable total (38.6%, with 61.4% unexplained), but the partition was markedly more confounded: only 10.6% of variation could be attributed uniquely to any one set, while 28.0% was shared among them. Each set explained a substantial amount on its own: depth and basin 0.264, hydrography 0.239, water-mass residence 0.222, fjord identity 0.143, yet hydrography and water-mass residence retained almost nothing independently. Fjord identity was the least redundant set (62% shared) and carried the largest unique fraction (0.054) despite explaining the least in total (**Online Resource 6**).

3.4.4 Concordance of taxonomic and functional composition

Mantel tests on Bray-Curtis vs Gower distances showed that taxonomic and functional dissimilarities were significantly correlated in all three ecological groups (all $p = 0.001$), but the strength of the relationship varied: correlation was roughly similar in the planktonic protist and zooplankton ($r = 0.57$ and 0.59, respectively), and strongest in the benthic macrofauna ($r = 0.76$).

4. Discussion

4.1 Physical isolation vs. Atlantic connectivity as a driver of biodiversity

The model results demonstrate that, despite being exposed to the same shelf water masses carried by the WSC, the two fjords represent very different types of hydrographic connectivity. In Kongsfjorden, Atlantic-derived water (AW/TAW) filled the basin along its entire length during every season, whereas in Van Mijenfjorden the basin remained dominated year-round by locally formed water masses with summer surface temperatures 1-2°C degrees cooler than surface temperatures at the same latitude outside the fjord on the shelf. The difference was equally evident in the flushing times, which were more than double in VMF than in KF, consistent with previous model results (Duarte et al. 2025). Both fjords showed a spring maximum in flushing times consistent with the onset of stratification suppressing exchange, but it was far more pronounced in VMF (53 days in April against 38 days in KF in May) and coincided there with melting seasonal ice. The mechanism is not simply a smaller opening; the model shows that due to the constriction the mean peak tidal surface currents in VMF were roughly six times stronger, and the gross transport through the two openings was comparable. What differed was that most of the water entering VMF on the flood was returned on the ebb within the same tidal cycle, so residual transport remained an order of magnitude lower. Moreover, the opening is shallow, so the entering water is drawn from the Intermediate Water laying at the surface, rather than the deeper Atlantic Water that ventilates KF. As such, both the quantity and the type of water that enters VMF from the shelf remains limited, whereas KF hydrographically functions essentially as an extension of the shelf system with direct connection to deep Atlantic water via the trough, with its water and the planktonic organisms suspended in it being renewed via advection on a time scale of roughly 10 days. In contrast, the flushing times in VMF were a month or longer, with little AW contribution, and local processes (sea-ice formation, freshwater input and atmospheric cooling) dominating water mass transformations.

Compared with this clear physical contrast, the biological differences between the fjords were modest. Fjord identity explained 4-9% of compositional variation in the plankton via PERMANOVA, and 14-15% in the benthic macrofauna. The absence of taxa exclusive to either fjord for any of the ecological

groups in the indicator analysis suggests that the connectivity to the open-shelf species pool is unlikely to be the main structuring mechanism (Węsławski et al. 2012), and differences present primarily as shifts in the relative dominance of taxa within a largely shared regional species pool rather than as complete species isolation, although the limited taxonomic resolution of our data could have obscured true species occurrences. Notably, in neither zooplankton nor benthic macrofauna did the colder, less Atlantic-influenced Van Mijenfjorden contain a higher proportion of Arctic taxa. This apparent mismatch between the physical and biological contrasts may be partly due to the fact that flushing rates describe the exchange of water, not of organisms. During the productive season, many zooplankton and meroplanktonic larvae concentrate in the upper water column, where they feed and develop (Patuła et al. 2026), and many taxa actively regulate their vertical position through swimming behaviour or buoyancy control (Bandara et al. 2021), regardless of which water mass they originated from. Because the shallow sill of Van Mijenfjorden draws its inflow from the surface layer, these surface-associated organisms are ones most likely to enter the fjord, even when Atlantic Water is excluded. Given its proximity to the Atlantic source on the shelf, even limited exchange may therefore be sufficient to supply much of the same regional species pool, making a physically restricted fjord considerably less isolated biologically. Conversely, taxa that overwinter at depth, such as diapausing *Calanus* spp., are likely to be more effectively excluded by the sill outside the productive season (Basedow et al. 2004), which would make biological connectivity of sill fjords both seasonal and taxon-specific.

For both planktonic protists and zooplankton, season accounted for much larger proportion of the variation than affiliation with a particular fjord, and differences between pelagic communities of the fjords were most evident in their differing seasonal dynamics. This was partially expected, as both communities undergo pronounced seasonal succession: protist assemblages shift from diatom-dominated spring blooms to flagellate- and mixotroph-dominated post-bloom communities over the course of the productive season (Hegseth et al. 2019), while zooplankton is governed by seasonally timed reproduction, recruitment and development (Søreide et al. 2022). The advective nature of Kongsfjorden was more evident in the low levels of seasonal variation in taxonomic and functional diversity of both planktonic protists and zooplankton, whereas in Van Mijenfjorden these metrics fluctuated significantly with season, resulting in contrasts between fjords observable only seasonally. Pelagic communities deviated most strongly between fjords during spring, coinciding with the season of weakest exchange and strongest hydrographic contrast: the flushing time of Van Mijenfjorden peaked at 53 days in April, while its basin remained capped by Winter-Cooled and Local Fresh Water masses beneath melting seasonal ice.

For protists, which can complete many generations even within the "short" Kongsfjorden residence time, this spring contrast likely reflected bloom phenology and local production, whereas for zooplankton, whose generation times are long relative to fjord flushing times but also undergo seasonal development, it is likely a combination of both. Our multivariate model results support this difference: for protists, the fitted hydrographic vectors aligned more closely with the seasonal axis of the ordination: surface temperature pointed into the summer and autumn Kongsfjorden quadrant, while surface salinity and stratification towards the spring, diatom-dominated one, so the measured hydrography largely described the seasonal cycle rather than any difference between fjords. For zooplankton, on the other hand, the hydrography vectors oriented along the fjord axis, suggesting that community differences in part reflected the hydrographic difference between the two systems. This is consistent with findings from western Norwegian fjords where the importance of advection relative to growth is much more pronounced in zooplankton compared to phytoplankton (Aksnes et al. 1989). For protists, the diatom-dominated quadrant of the ordination also held the Arctic Water and Winter-Cooled Water centroids, tying the assemblage directly to the locally formed, ice-influenced water masses that are characteristic of Van Mijenfjorden in spring. By summer, the differences between fjords in both protist and

zooplankton communities were weaker, and by autumn they largely disappeared as the Van Mijenfjorden community developed, coinciding with the annual minimum in flushing times (19-21 days in September-November). This seasonal convergence closely parallels the phenological lag documented between Kongsfjorden and the ice-covered Rijpfjorden, where zooplankton communities were comparable in winter but diverged in spring and summer (Weydmann-Zwolicka et al. 2021) with a lag of 2-3 months, such that the autumn communities in Rijpfjorden resembled the summer communities in Kongsfjorden. Similarly, a previous study found the protist communities in Van Mijenfjorden to be delayed relative to Kongsfjorden in spring/early summer (Smola et al., in revision). This suggests that physical isolation appears to act on the pelagic communities mostly by delaying phenology and shifting the relative dominance of advected versus resident species, rather than resulting in the exclusion of taxa entirely, and critically highlights the importance of taking phenology into account when conducting comparative studies between fjord systems.

In contrast, the fjord effect accounted for approximately twice as much variability in taxonomic or trait composition of benthic macrofauna compared with planktonic protists or zooplankton. This likely reflects larval dispersal capacities of benthic fauna and the influence of water mass residence times within the fjords. Most benthic species are only capable of long-distance dispersal during their planktonic larval phase, if at all, whereas planktonic communities are repeatedly redistributed by water movement. As such, dispersal limitation can contribute to differentiating communities between neighboring fjords or even among basins within the same fjord (Kokarev et al. 2024, 2025). At the same time, many meroplanktonic larvae occur in the surface layer during the productive season (Patuła et al. 2026), so larval supply to a sill fjord close to the Atlantic source may be less restricted than water-mass exchange alone would suggest. The strong along-fjord patterns of taxonomic and trait composition of benthic macrofauna therefore cannot be attributed to connectivity alone, but also reflect environmental conditions associated with glacial processes (Renaud et al. 2007; Włodarska-Kowalczuk et al. 2012; Węsławski et al. 2012). Our environmental analysis points in the same direction. Station position (depth and fjord basin combined) was both the largest and the least redundant contributor to benthic taxonomic composition, and the ordination was most strongly correlated with water depth and with the duration of Atlantic Water influence, which are precisely the axes along which the model output separated the two systems. Kongsfjorden was close to uniform in summer surface temperature along its entire length and ventilated by AW/TAW throughout, whereas there was a pronounced temperature gradient in Van Mijenfjorden, with no Atlantic-derived water anywhere beyond the sill. The benthic communities reproduce this asymmetry: Van Mijenfjorden stations separated into three groups along the fjord axis, whereas in Kongsfjorden the dominant gradient was depth rather than along-fjord position, and the deeper Kongsfjorden stations clustered with the Van Mijenfjorden shelf stations. As such, the benthos tracked the along-fjord hydrographic gradients shown by the model, and where they showed uniformity, the benthos was organised by depth instead.

Even after accounting for all measured hydrographic variables, fjord identity and season/fjord basin, 59-77% of the compositional variation remained unexplained by the constrained multivariate models for all ecological groups. Such low explained inertia values should not on their own be interpreted as evidence of model failure: constrained ordinations of large, zero-inflated community matrices containing many rare and patchily distributed taxa rarely explain more than a modest proportion of the total variation (Økland 1999). In our case, several factors likely contributed to this residual variation, most notably, a limited set of predictors that excluded nutrients, light, oxygen, sea-ice conditions, grazing and other biological interactions, and the advective history of the sampled water. Our data also included only a few sampling years, particularly in Van Mijenfjorden, so interannual variability could not be properly accounted for, and likely makes up a large part of the residual variation. Long-term monitoring in Kongsfjorden has shown that interannual variability is substantial for both planktonic

groups (Hop et al. 2019b; Assmy et al. 2023). Finally, stochastic variation and small-scale patchiness (Mackas et al. 1985), which is a general problem in marine ecology, where a single sample at one point in time is assumed to represent a larger area, likely added to variation that no set of predictors could explain. The low proportion of explained variation is thus a reflection of the limited nature of the compiled data at least as much as the ecology of the two fjords, and the small fractions attributed to fjord identity should be regarded as approximate. On the other hand, the collinearity among many of our variables, e.g., depth, bottom salinity and Atlantic Water residence time in the benthic dataset, is not incidental: deeper stations are those with access to the denser, saltier, Atlantic-derived water that the sills would exclude from shallower basins. As such, the heavily shared variance partitions in most of our datasets is the expected consequence of a single physically structured gradient rather than a shortcoming of the analysis.

4.2 Functional vs. taxonomic diversity

Taxonomic and functional diversity metrics capture different yet complementary properties of a community. Including both documents taxonomic variability while providing insight into the consequences of these differences in time or space and allows to visualise whether observed contrasts are expressed only in the taxonomic or functional component, or in both. A shift in both components of diversity suggests a compositional change with functional consequences, whereas a difference in only the taxonomic component suggests redundancy, where function is preserved despite changing species composition. In our study, the former was evident most clearly in the Van Mijenfjorden zooplankton richness, where the seasonal increase in species richness from spring to summer clearly tracked functional richness, indicating that the spring community was not only species-poor but also had a limited functional capacity. For evenness, however, the two were decoupled, with a significant summertime drop in taxonomic but not functional evenness, and the resulting difference between fjords was visible only in the taxonomic component. One explanation is that the few numerically-dominant taxa in Van Mijenfjorden were functionally distinct from one another, such that abundance remained evenly spread across traits despite being concentrated in fewer species. In contrast, for benthic macrofauna of the outer basins, the differences between fjords were mirrored in both diversity components: taxonomic and functional evenness were both higher in Van Mijenfjorden at comparable richness of either kind, suggesting that the two fjords host similar numbers of taxa spanning similar traits, but that abundance in Kongsfjorden is concentrated into fewer taxa which exhibit fewer trait combinations (i.e. an uneven distribution of abundance by traits).

For planktonic protists, most taxonomic and functional diversity metrics did not differ between the fjords (the exceptions being species richness in spring and functional evenness in autumn), and composition differed only weakly, with unequal multivariate dispersion making the taxonomic contrast difficult to interpret. Season-averaged trait composition nevertheless suggested that diatoms, phototrophs, larger cells and ice-associated taxa were more prominent in Van Mijenfjorden, and flagellates, mixotrophs and nano-sized cells in Kongsfjorden (Figure 7a). As these averages pool samples across seasons, they may be influenced by differences in seasonal sampling coverage between the fjords, and are best interpreted together with the spring-dominated contrast described above. The similarity of diversity metrics despite some compositional differences is consistent with a degree of functional overlap among protist taxa, but also partly reflects the coarse trait information available for protists (five traits with few modalities), which limits the ability of functional metrics to discriminate between communities, as well as the limited taxonomic resolution of light microscopy for small protists.

At the community level, taxonomic and functional dissimilarities were correlated in all three ecological groups, but most strongly in the benthic macrofauna. The weaker correlation in the plankton

suggests that compositional turnover there is only partially translated into shifts in trait composition, consistent with some functional redundancy among co-occurring taxa, whereas in the benthos differences in species composition were more consistently accompanied by differences in traits. Functional redundancy may provide resilience to the ecosystem against climate perturbations or other anthropogenic stressors if key functions can be maintained with altered taxonomic composition (Wlodarska-Kowalczuk et al. 2012). However, there is also evidence that benthic macrofauna communities here utilize resources similarly despite differences in taxonomic or trait composition (Wlodarska-Kowalczuk et al. 2019). Therefore, it is important to distinguish between spatial patterns in overall functional capacity of a community or specific functional roles, such as in trophic interactions or carbon cycling, which may not follow the same patterns. Whether the redundancy suggested by our trait-based metrics implies that ecosystem functions would be maintained under continued Atlantification, therefore, cannot be assessed with the present data.

4.3 Challenges, study limitations and future directions

Our data highlight three main challenges inherent to any comparative study spanning multiple habitats and trophic levels, which also represent practical priorities for future monitoring efforts: resolving seasonal timing, disentangling the drivers of phenological shifts, and matching sampling resolution to the different response timescales of pelagic and benthic communities. The contrasts we observed, or failed to observe, between the fjords repeatedly highlight the importance of seasonal timing for conducting comparative studies between systems, and for tracking ongoing Atlantification in the pelagic realm. Depending on whether sampling took place in spring or later in the season, a comparison of protist species richness would have indicated either higher richness in Kongsfjorden or no significant difference between the fjords. As such, single-season surveys may overestimate or miss differences between fjords, and sampling designs need to resolve the seasonal cycle to distinguish shifts in phenology from changes in community composition. Autonomous samplers such as the RAS deployments (Smola et al., in revision) and included here provide one practical means of achieving this in less accessible areas.

Seasonal timing is not only a sampling concern, but a response in its own right. Our results suggest that for the plankton, one of the most readily detectible consequences of increasing Atlantification may be a change in phenology, which will also affect the timing of food availability for higher trophic levels and to the benthos. However, attributing phenological shifts to AW alone is not straightforward. Long-term observations from Kongsfjorden show that the relationship between AW inflow and bloom phenology depends on how and when AW enters the fjord (Hegseth and Tverberg 2013): both during ice-covered and ice-free years but with AW inflow along the bottom, winter convection allowed the diatom-rich spring bloom to occur on time, whereas in ice-free years when AW entered the fjord in the surface layer, it suppressed winter mixing and resulted in a later bloom with lower biomass and diversity (Hegseth and Tverberg 2013). Bloom timing and the seasonal succession of zooplankton are also shaped by factors that were not measured in our data, including sea ice history, freshwater and glacial runoff, nutrient supply and biological interactions like grazing pressure, predation and timing of reproduction of key species. Advections of populations with different seasonal timing from the shelf could further blur local phenological signals. As sea ice declines, the difference in bloom timing between open and sill-restricted fjords may therefore change, although not necessarily in a predictable direction. Sill fjords such as Van Mijenfjorden may shift towards earlier blooms as ice retreats earlier, while open fjords such as Kongsfjorden may shift towards later ones if surface AW increasingly suppresses winter mixing. Separating these mechanisms will require seasonal plankton monitoring paired with concurrent observations of sea ice, winter mixing and the depth of AW inflow, as partially achieved in the Kongsfjorden pelagic monitoring programme.

A third challenge is matching sampling resolution to the time- and spatial scales over which different ecosystem components respond, as well as reconciling data that integrate change over such different timescales. There is a mismatch between the rapidly changing environmental conditions occurring within the pelagic realm and life history characteristics of benthic fauna, which makes it difficult to detect ecosystem-wide temporal changes. For instance, temporal studies of benthic macrofauna in Kongsfjorden have shown insignificant seasonal changes in abundance, biomass and individual body sizes (Kędra et al. 2012; Włodarska-Kowalczuk et al. 2016) but major species compositional shifts have been observed over a decade (Kędra et al. 2010). In Van Mijenfjorden, minimal compositional change was observed over two decades (Renaud et al. 2007). In this way, benthic macrofauna integrates the cumulative hydrographic, sedimentary and disturbance regimes of each fjord over years to decades while pelagic organisms better reflect seasonal conditions as they respond over days to years. The systematic seasonal pelagic monitoring of Kongsfjorden (Hop et al. 2019b; Wold et al. 2024a) has greatly improved the understanding of how trends in climatic conditions affect the pelagic ecosystem and food web. However, without similar monitoring of benthic conditions and assemblages, and within fjords of contrasting climatic changes, comparison of independent studies remains the only practical approach for detecting temporal change. Thus, future monitoring efforts in Svalbard fjords should prioritise high temporal resolution, ideally with seasonal and year-round sampling coverage, and complimentary temporal sampling covering pelagic and benthic ecosystem components.

The interpretation of our results is constrained by several significant limitations. Since the present study was conducted from a compilation of independent datasets, differences in sampling and processing methods may have partially conflated the results. With the exception of one dataset each for planktonic protists and benthic macrofauna, every data source in our compilation covered only one of the fjords, and the sources often varied slightly in their sampling gear, sample processing procedures and taxonomic resolution. Mesh and sieve size can affect estimates of abundance, biomass, and taxon richness, particularly for small-bodied taxa (Gage et al. 2002; Thompson et al. 2003; Riccardi 2010), and taxonomic expertise can vary substantially between labs. Taxonomic harmonisation to the lowest common resolution, as applied here, reduces, but does not remove, these effects, and comes at the cost of taxonomic detail. Because methodological differences may have either inflated or obscured real differences between the fjords, the contrasts reported here cannot be fully disentangled from their data source and should therefore be interpreted with caution. Reassuringly, however, the two datasets that did span both fjords, which were sampled with consistent gear and processed by the same analysts, showed the same between-fjord trends as the compilation as a whole, supporting the interpretation that at least part of the observed differences reflect genuine ecological contrasts rather than artefacts of data source alone.

Data coverage between fjords was also vastly uneven, especially for protists and zooplankton, where long-term high-quality seasonal data was available from Kongsfjorden, but in Van Mijenfjorden was confined mainly to just two years, namely 2016-2017, and were also the years that the model simulated. These were unusually warm years with limited sea-ice cover compared with long-term conditions (Cullather et al. 2016; Overland and Wang 2016). As such, both hydrographic and biological differences between the fjords may be greater in colder years with more extensive sea ice, although we cannot test this with the present data. More generally, the small number of sampling years in Van Mijenfjorden means that we could not separate interannual variability from seasonal or between-fjord differences, so the seasonal patterns described here may partly reflect conditions in particular years. Apart from one dataset that was obtained from autonomous samplers in both fjords, plankton samples covered only March-October; even within the latter dataset the winter samples were biased by a very small sampling volume that was not sufficient to reliably collect a representative sample of a low-

density winter protist population, leaving the polar night mostly unrepresented. Benthic samples collected between 2007 and 2023 were related to environmental conditions from a single modelled year, which assumes that differences among stations are stable over time. The scarcity of data from Van Mijenfjorden also prevented the inclusion of fish and marine mammals, although predation by juvenile boreal fish such as Atlantic cod and haddock, currently abundant in Kongsfjorden, could contribute to differences in zooplankton communities between the fjords (Renaud et al. 2012), and these groups represent a strong interest both scientifically and for sustainable management.

Taxonomic resolution was also limited by reliance on morphological identification, particularly for small protists or meroplankton, which often cannot be reliably resolved by light microscopy, and further reduced by the need to harmonize data to the lowest common denominator. Biogeographic structure in Svalbard fjord protist communities has been previously resolved successfully using molecular data (Šupraha et al. 2022), and molecular approaches like metabarcoding would allow more consistent comparisons across sites and data sources. Trait information was also incomplete for some taxa, and very coarse for protists, limiting the resolution of the functional analyses.

Given these limitations, future comparative studies would benefit from coordinated sampling of contrasting sites within the same years and seasons, using harmonised protocols and clearly documented taxonomic conventions, and more complete trait information. Additionally, incorporating information on biological interactions such as predation, competition, and other top-down controls and on environmental controls of physiology and life history would help move the field from purely descriptive comparisons towards understanding the mechanisms that generate them.

4 Summary

This comparative study has shown that the direct and indirect effects of hydrography in two fjords with contrasting advective regimes variably influenced different ecological groups. Within planktonic communities, the clearest differences between the fjords were reflected in the phenology, resulting in strongest differences during spring that diminished as the season progressed. While no taxa were identified to be exclusive to either fjord, the zooplankton composition differed in a way consistent with the source of AW: Kongsfjorden held more large, carnivorous, oceanic and Atlantic taxa, while Van Mijenfjorden had more small, neritic copepods, although the share of Arctic taxa was similar in both fjords. Planktonic protist communities differed only weakly between the fjords and were structured mainly by seasonal succession, but Van Mijenfjorden held a greater share of diatoms and ice-associated taxa, consistent with its colder, locally formed water masses, whereas Kongsfjorden had more flagellates, mixotrophs and nano-sized cells. Macrobenthic communities showed the strongest fjord contrast, although it was partially confounded by depth and along-fjord gradients. Taxonomic and functional composition were also more tightly coupled in the benthos than in the plankton, suggesting greater functional overlap among planktonic taxa. Together, these results highlight that pelagic and benthic communities respond to differences in fjord connectivity in different ways, which can broadly be related to water mass distributions, life-history traits that affect dispersal capacity, including vertical positioning and seasonal use of surface waters. This study also highlights the challenge in comparing multiple community types using unbalanced and limited data from multiple sources, where sampling bias is hard to separate from biological signal. To capture the effects of ongoing Atlantification, future studies should aim to establish coordinated, ecosystem-wide, seasonally resolved sampling with harmonised methods across multiple contrasting fjords and years.

5 Statements and Declarations

Competing Interest

Ethical approval: No animal testing was performed during this study.

Conflict of Interest: The authors declare that they have no conflict of interest.

Data availability: All previously published data have been cited and are made publicly available by original authors. Data that were unpublished at the time of this study can be made available upon request to the authors.

Author contributions: EL, AZ, SM, EEM, and PER conceived the study. EEM, AZ, SM, IYU, EL, and MB contributed to data compilation. Data were contributed by EL, PA, HH, MK, JL, BO, PER, JES, ET, MWK and AW. MB conducted modelling analyses together with AB. Model setup and run were by MB, AB. EEM and AZ conducted statistical analyses. EEM, AZ, EL, MB wrote the manuscript and all authors contributed to reviewing, editing and approval of the final version.

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Tables and figures

Table 1. Data sources used in the study

Community	Fjord	Years sampled	No. sites	No. stations	Citation(s)
Phytoplankton	Van Mijenfjorden	2015-2017	7	36	(Leu et al. 2020)
	Kongsfjorden / Van Mijenfjorden	2015-2016	2	44	(Smoła et al. in revision)
	Kongsfjorden	2009-2013	2	11	(Hegseth et al. 2019)
	Kongsfjorden	2014-2022	6	98	(Assmy et al. 2023; Wold et al. 2024a)
Zooplankton	Van Mijenfjorden	2022	5	5	(Trudnowska et al. 2026)
	Kongsfjorden	2015-2024	6	147	(Hop et al. 2019b; Wold et al. 2024b)
	Van Mijenfjorden	2015-2017	5	23	(Cuny 2017; Svendheim 2017)
Benthos	Kongsfjorden	2021-2023	7	7	(Christensen et al. 2024)
	Van Mijenfjorden	2007-2014	12	12	(Velvin and Evenset 2008; Velvin et al. 2014)
	Kongsfjorden	2012-2013	3	10	(Włodarska-Kowalczuk et al. 2016)
	Van Mijenfjorden	2016	1	1	(Oleszczuk et al. 2021)
	Kongsfjorden	2013	3	3	(Zaborska et al. 2018)
	Kongsfjorden	2009	8	8	(Kędra et al. 2011, 2026)
	Van Mijenfjorden	2019	5	5	Unpublished (Maria Wlodarska-Kowalczuk)

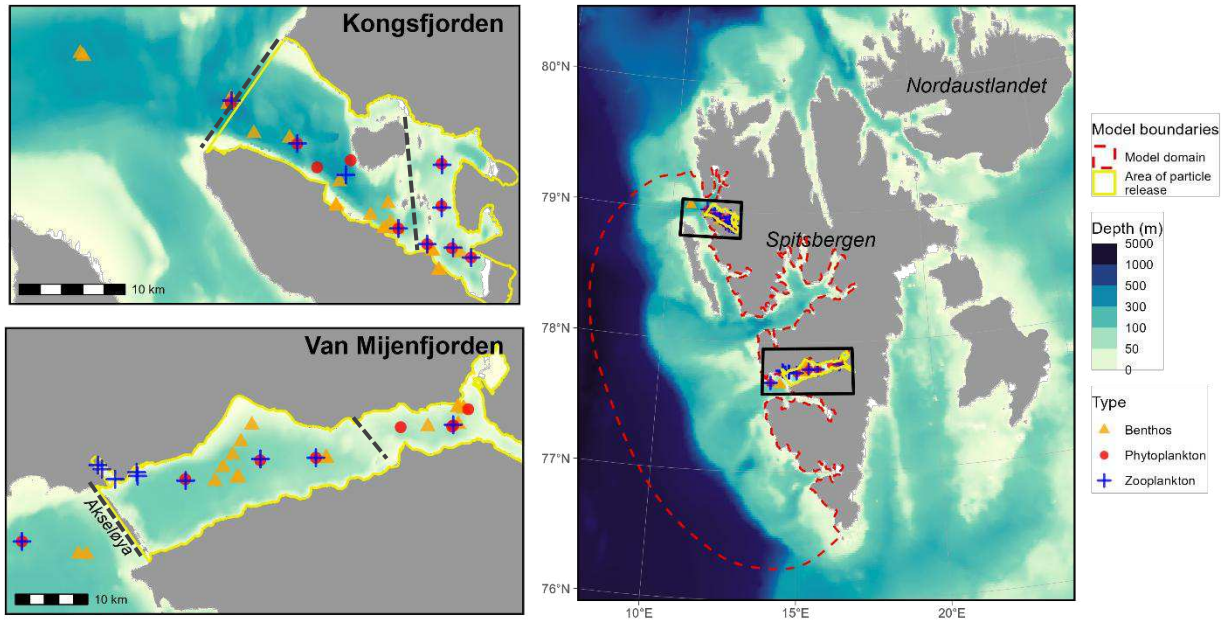


Figure 1 Overview of Kongsfjorden and Van Mijenfjorden in Svalbard (right) with sampling locations of planktonic protists (phytoplankton, red circles), zooplankton (blue crosses) and benthic macrofauna (benthos, orange triangles) from data compilation shown (left). Red dashed line shows model boundary; yellow solid line shows the area used for particle release. Black dashed lines show the separation between inner and outer fjord basis while any samples outside of the fjords occupy the shelf.

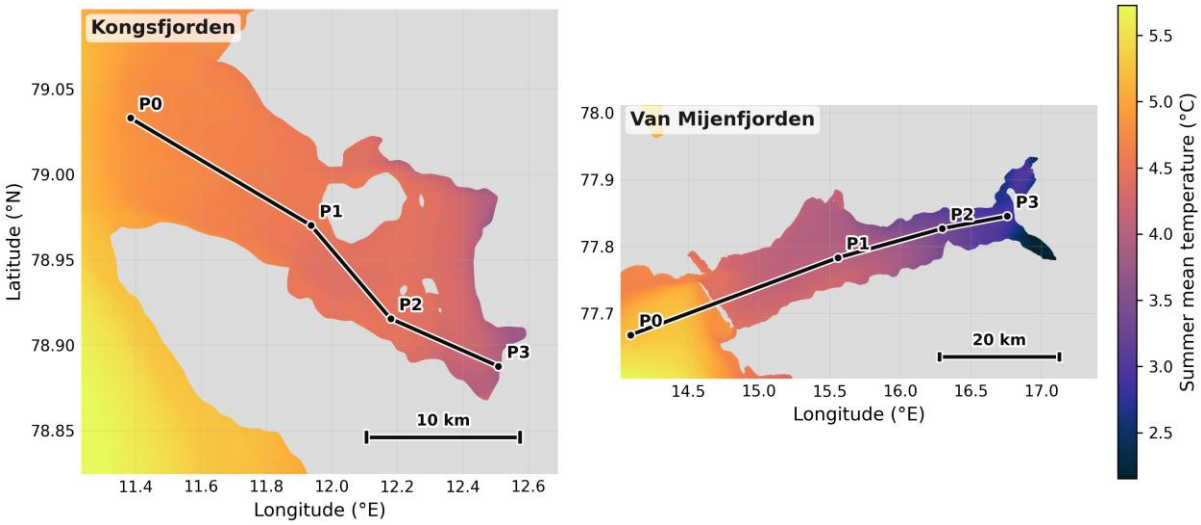


Figure 2 Mean Summer (JJA) surface temperature in Kongsfjorden and Van Mijenfjorden. The transects P0 – P3 correspond to transects in Figure 3. Note the difference in scale between the two fjords.

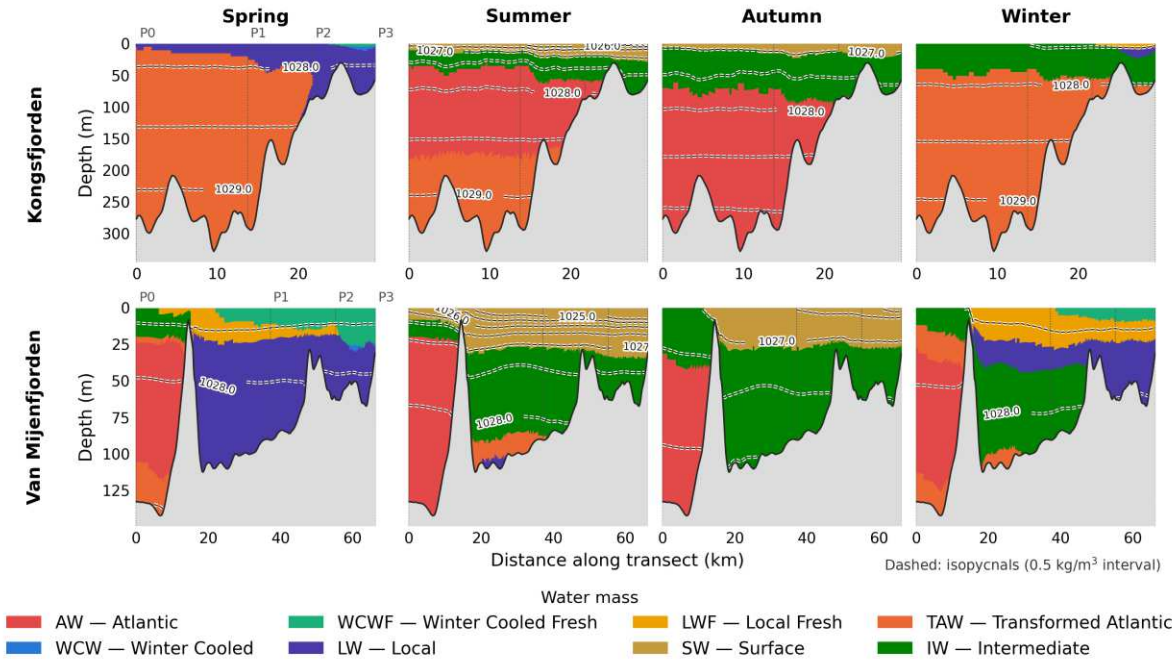


Figure 3 Seasonal presence of different water masses in Kongsfjorden and Van Mijenfjorden along the transects shown in Figure 2. Water mass definitions are from Cottier et al. (2005). Seasons are defined as Spring (MAM), Summer (JJA), Autumn (SON), Winter (DJF). Note the different scales along the x axis.

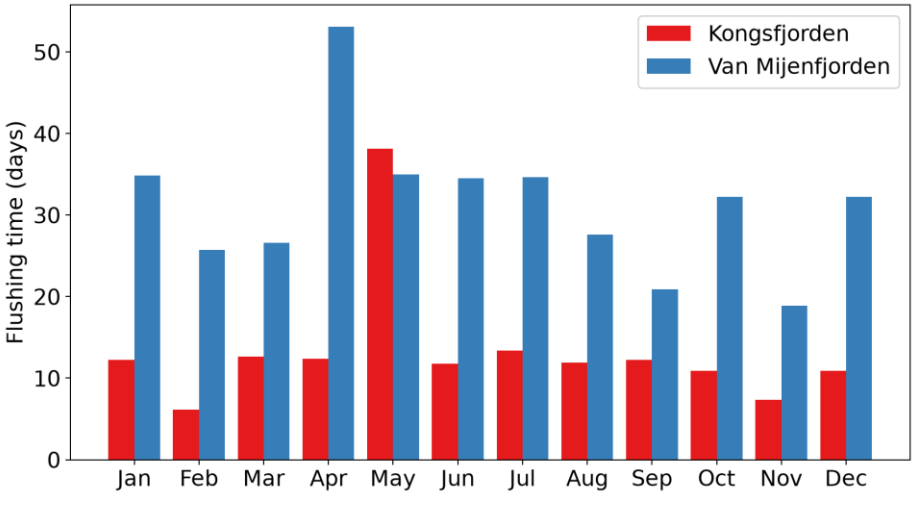


Figure 4 Flushing time in days for Kongsfjorden (red) and Van Mijenfjorden (blue) for each month in the model.

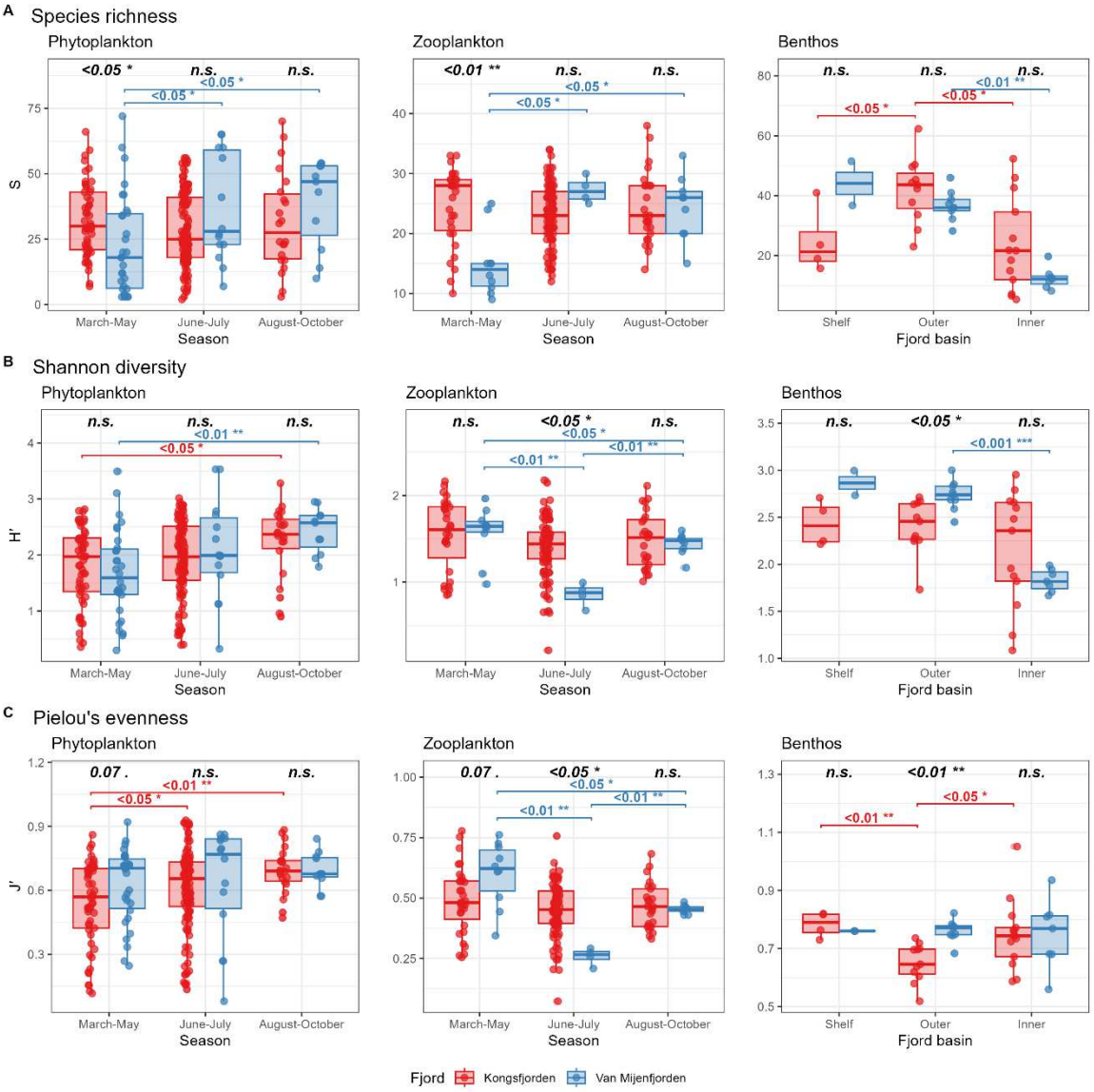


Figure 5 Station-level taxonomic diversity metrics. (A) species richness, (B) Shannon diversity (B) and (C) Pielou's evenness calculated for communities of planktonic protists (phytoplankton), zooplankton, and benthic macrofauna (benthos) in KF (red) and VMF (blue). Metrics are shown across seasonal groupings for phytoplankton and zooplankton, and across fjord basis for benthos. Significance (p_{adj}) of differences between seasons or basins within each fjord are shown with horizontal bars (only significant differences shown) and between fjords on top of the plots in black; n.s. – not significant ($p > 0.1$); – $p < 0.1$ * – $p < 0.05$** – $p < 0.01$**, $p < 0.001$***.

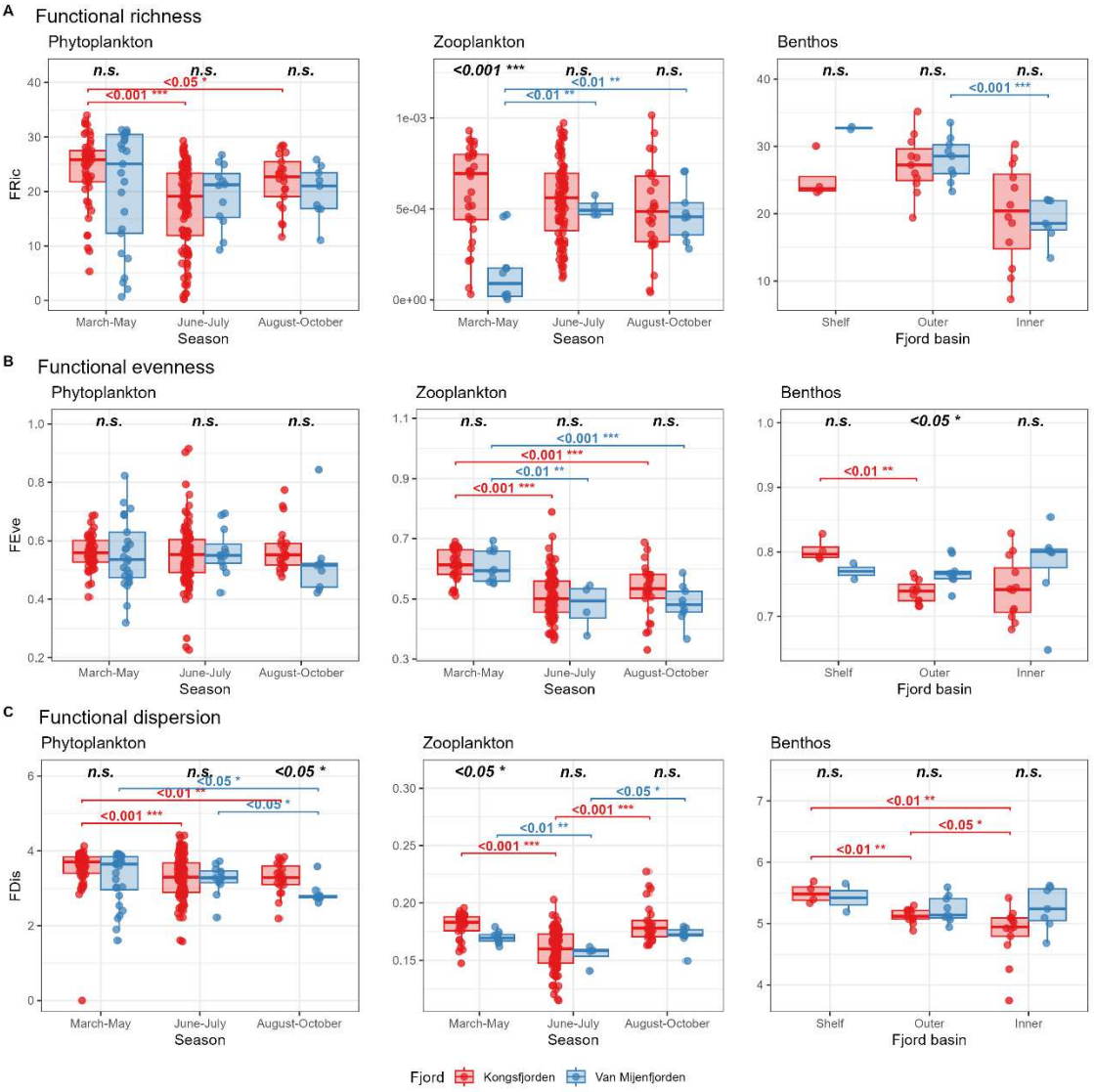


Figure 6 Station-level functional diversity metrics. (A) functional richness (FRic), (B) functional evenness (FEve) (B) and (C) functional dispersion (FDis), calculated for communities of planktonic protists (phytoplankton), zooplankton, and benthic macrofauna (benthos) in KF (red) and VMF (blue). Metrics are shown across seasonal groupings for phytoplankton and zooplankton, and across fjord basis for benthos. Significance (p_{adj}) is shown on top of the plots; n.s. – not significant ($p > 0.1$) – $p < 0.1$* – $p < 0.05$** – $p < 0.01$- $p < 0.001$***

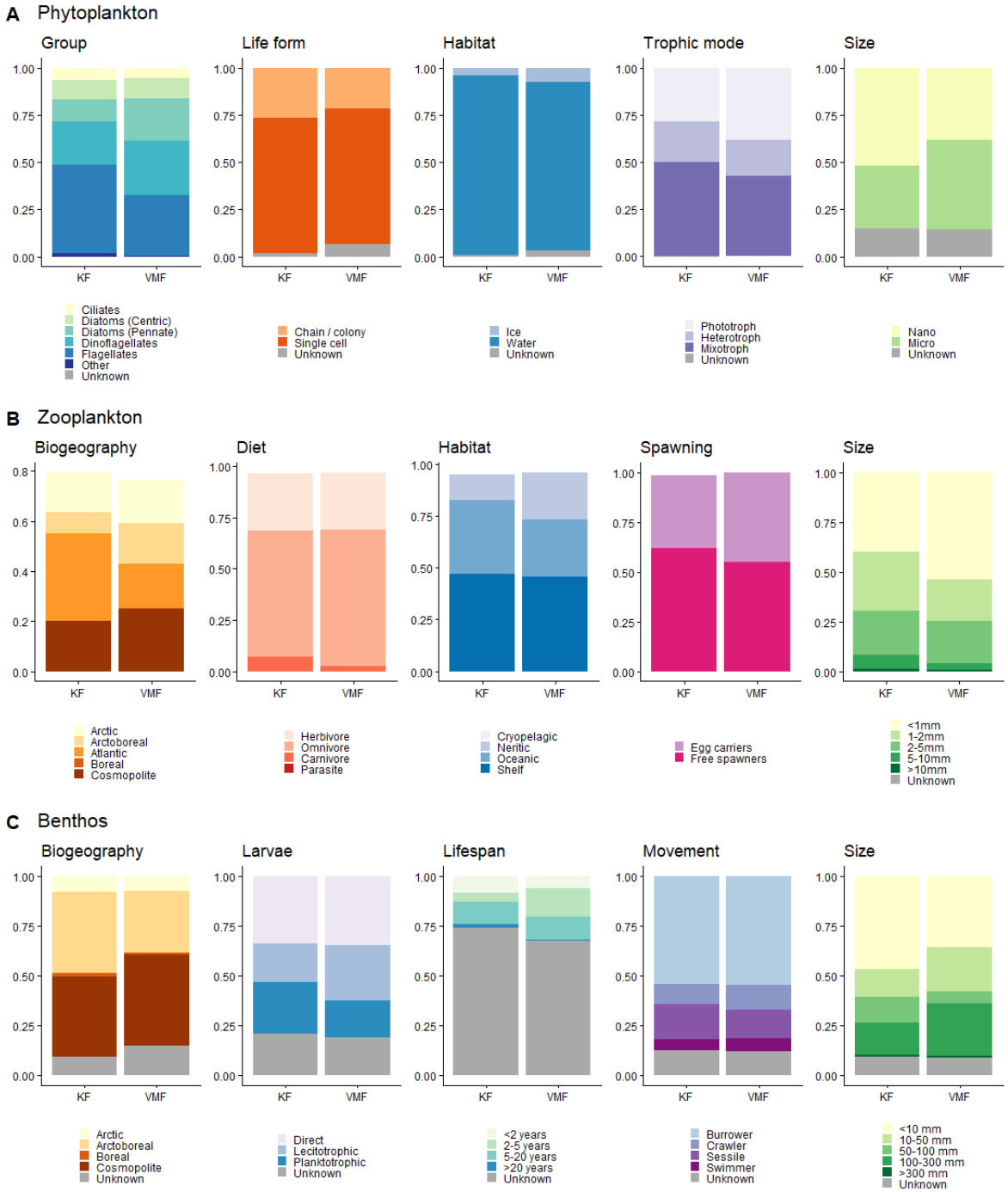


Figure 7 Mean contributions of selected traits to total abundances in samples from Kongsfjorden (KF) and Van Mijenfjorden (VMF) for (A) planktonic protists (phytoplankton), (B) zooplankton and (C) benthic macrofauna (benthos). Data is averaged across seasons and fjord basins.

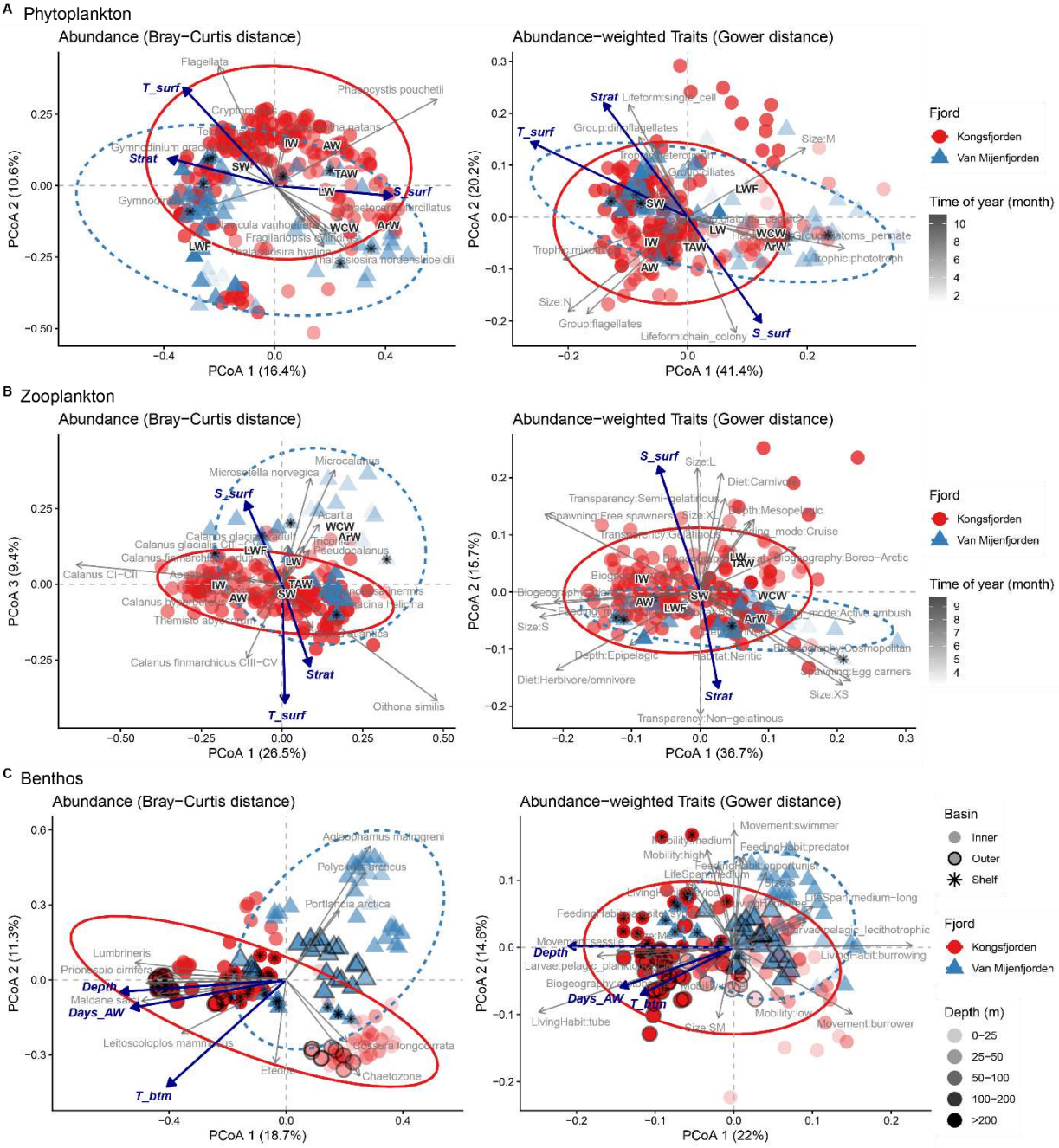


Figure 8 Principal Coordinates Analysis (PCoA) of Hellinger-transformed abundances (left) and abundance-weighted traits (right) for planktonic protists (phytoplankton, A), zooplankton (B) and benthic macrofauna (benthos, C). For all plots, points represent samples with the color and shape indicating fjord while shading indicates time of year samples were collected (phytoplankton and zooplankton) or sampling basin (benthos). Ellipses contain 95% of the data and gray vectors show taxa or traits that were significantly associated with the two PCoA axes shown, with the length of the vector reflecting fit (R^2). Asterisks show shelf stations located outside the fjord mouth. Bold black text labels indicate centroids for surface water mass; abbreviations as in Figure 3. Blue vectors and text indicate environmental variables significantly correlated with the ordination, with length of the vector reflecting fit (R^2); T_surf – surface temperature; S_surf – surface salinity; T_btm – bottom temperature; Strat – stratification index; Days_AW – days per year bottom water layer occupied by Atlantic Water; Depth – bottom depth.

Supplementary Files

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- SupplementaryMaterial.docx