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Surveying marine biodiversity using eDNA metabarcoding of seawater and sediment in a high Arctic fjord during the polar night (Kongsfjorden, Svalbard)

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ABSTRACT

The marine ecosystem of Kongsfjorden (KF), Svalbard, is directly affected by ongoing climate change in the Arctic. Shifts in species composition and distributions are already underway as a result of the transition from Arctic to Atlantic conditions in the fjord. The polar night is a period of challenging conditions and is historically understudied, and thus our understanding of the biodiversity of major eukaryotic groups is particularly limited at this time of year. Here we aimed to provide a comprehensive snapshot of eukaryotic biodiversity present in KF during the polar night using environmental DNA (eDNA) metabarcoding of the mitochondrial cytochrome *c* oxidase subunit 1 gene (COI). Additionally, we sought to establish a baseline dataset for gelatinous zooplankton (GZP) during this period by combining eDNA with net sampling. Lastly, we tested for the impact of PCR-inhibition on the recovery of eDNA from turbid fjord waters. We successfully generated species lists for a large component of the pelagic community known to inhabit KF, benthic and hyperbenthic species typical to the area, as well as a number of new detections. We recovered taxa from major functional groups in the fjord, including macroalgae, phytoplankton, zooplankton, large vertebrates and benthic invertebrates. Finally, we recovered a richer polar night GZP community than previously detected with morphology-based methods, including other seasons. This study demonstrates the versatility of eDNA metabarcoding for marine biodiversity surveys in challenging environmental conditions and provides a baseline for future polar night eDNA-based biodiversity monitoring in KF.

1. Introduction

Effective biodiversity monitoring is crucial to understanding ecosystem health and detecting the impacts of climate change on marine ecosystems. Detailed data on species distribution and abundance in relation to their environment is necessary for detecting shifts in biodiversity and therefore making informed management and mitigation decisions. Biodiversity assessments are often highly dependent on morphological identification and while this remains a valuable tool, it comes with drawbacks and limitations that mean sample collection can outpace sample processing (Porter and Hajibabaei, 2018). For example, taxonomic identification requires expert knowledge which can be scarce and difficult to access (Paknia et al., 2015). Additionally, it is crucial that specimens are well-preserved after sampling and have visually identifiable characteristics. However, collecting organisms for such identification is often invasive, impacting fragile organisms, and can overlook difficult to detect life stages such as larvae. All of these factors can reduce the cost and time-effectiveness (Pawlowski et al., 2022), and in turn limit their usefulness for early detection of the biological impacts of rapidly changing environmental conditions in areas such as the Arctic. Advances in molecular (meta)barcoding can complement information gained through morphological work by circumventing some of these limitations, as well as providing the opportunity to increase sampling coverage over space and time while reducing costs per sample (Porter and Hajibabaei, 2018). One such tool that has become a popular tool in biodiversity monitoring in the last decade is environmental DNA

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(eDNA) metabarcoding, which relies on the isolation of DNA from environmental samples such as water or sediment. It is composed of DNA shed by organisms (e.g., metabolic waste products, shed cells, gametes and mucus) as well as whole organisms themselves in the case of small taxa (e.g., diatoms and microscopic meiofauna). After isolation, eDNA can be sequenced using Next Generation Sequencing (NGS) technology and subsequently compared to reference databases, producing taxon data. It is increasingly being implemented in remote systems such as the Arctic, including in coastal waters (Lacoursière-Roussel et al., 2018; Leduc et al., 2019), surveying pelagic and deep-sea metazoans in the open ocean (Murray et al., 2024), under-ice communities in the marginal ice zone (Murray et al., 2025) and benthic communities in fjords (van den Heuvel-Greve et al., 2021; Willassen et al., 2022).

Fjord systems are highly productive components of the Arctic marine realm and thus are important habitats to numerous species, some of which are endemic. As transition zones between land, glaciers and ocean, Arctic Fjords are particularly vulnerable to the impacts of anthropogenic climate change (reviewed in Bianchi et al., 2020). Indeed, Arctic warming is occurring up to four times faster than the global average in a phenomenon known as Arctic Amplification (Cohen et al., 2020; Isaksen et al., 2022; Rantanen et al., 2022). The Svalbard Archipelago is situated on the eastern side of Fram Strait in the European Arctic and its western fjords are particularly vulnerable to Atlantification, which describes the process of physical conditions, as well as biological communities, becoming more like those in the North Atlantic (Ingvaldsen et al., 2023; Polyakov et al., 2020, 2023). The West Spitsbergen Current (WSC), which transports warm and saline waters of Atlantic origin northward through Fram Strait and into the Arctic basin, has continuously warmed over the last decades, resulting in Fram Strait and western Svalbard becoming increasingly Atlantified (Cottier et al., 2005; Ingvaldsen et al., 2023; Polyakov et al., 2023). Kongsfjorden (KF) is an open fjord located on the north-west coast of Svalbard, and is at the interface between high-Arctic and sub-Arctic marine biogeographic regions (Bischof et al., 2019). The impacts of ongoing warming are evident year-round in the region, but are particularly strong in the winter period (Francis and Vavrus, 2012; Pithan and Mauritsen, 2014). Higher temperatures during the polar night and winter prevent water from cooling to freezing temperature, resulting in less sea ice formation in the coldest months. Indeed, land-fast ice has rarely occurred in KF since the abnormally warm winter of 2005/06 (Cottier et al., 2007, 2019; Gerland et al., 2020).

The hydrographic conditions in KF have significant impacts on the local ecosystem, influencing the biomass and community composition of zooplankton (Basedow et al., 2004; Gluchowska et al., 2016), primary production (Dragańska-Deja et al., 2024; Hegseth et al., 2019), and larger vertebrates such as fish and marine mammals (de Vincenzi et al., 2019; Marques et al., 2023). The influence of both Atlantic and Arctic water masses means that KF harbours communities that are a combination of arctic, arctic-boreal and boreal biogeographic origin. In years when higher levels of Atlantic water masses are advected into the fjord, for example, the zooplankton community is likely to be dominated by boreal species, and the opposite is true in years where Arctic water masses prevail (Dalpadado et al., 2016; Gluchowska et al., 2016). Major changes in abundance and community composition have been already observed or are predicted to occur in many key functional groups including macroalgae (Düsedau et al., 2024), crustaceans (Hop et al., 2019; Węsławski et al., 2018), and fish (Gorska et al., 2023). Another group predicted to undergo major shifts due to changing conditions in the Arctic is gelatinous zooplankton (GZP), defined here as the pelagic life stages of cnidarians, tunicates and ctenophores. They have remained understudied until recent years, despite having major roles throughout pelagic food-webs as filter feeders (e.g., Stukel et al., 2024), predators (e.g., Hansson et al., 2005; J. E. Purcell et al., 2010) or as prey (Dischereit et al., 2024a, 2024b). Furthermore, species distribution models have predicted that the distribution of many GZP species is likely to expand significantly poleward as a consequence of climate change, while some others will experience range contractions (Pantiukhin et al., 2024). There remain large gaps in baseline data regarding the distribution and community composition of these groups during the polar night.

One of the most characteristic features of high-latitude systems such as KF is their strong seasonality. The Arctic “polar night” occurs during the winter season and is typically characterised by the sun remaining below the horizon for 24 h per day and consequentially low (although not devoid of) incoming light levels. Thus, the polar night has traditionally been considered as a period of dormancy in the Arctic due to low light and food availability. It was assumed that biological activity dropped to negligible levels and thus not considered as important to research compared to other, highly productive periods (Berge et al., 2020b). Nevertheless, other physical processes occur during this period including increased vertical mixing in the water column and cooling of the surface layers. The coldest surface temperatures typically occur after the polar night in March and April, where freezing and sea-ice formation is the most likely to occur (Cottier and Porter, 2020). Due to these aforementioned physical properties, sampling during the polar night is also constrained by technical and logistical challenges and this season therefore remains a relatively understudied aspect of the Arctic ecosystem (Berge et al., 2020b). A growing body of research in the last decade has found that the polar night is not only highly productive across trophic levels, but also crucial to our understanding of Arctic ecology and understanding the ongoing impacts of climate change (Berge et al., 2015a, 2015b; Grenvald et al., 2016; Last et al., 2016).

Another key feature of KF, and other Arctic fjords, is that they can have high levels of suspended organic and inorganic particles present in the water column as a result of glacier discharge, river runoff and snow and permafrost melt. Discharge from the tidal glaciers at the head of KF increases water turbidity and sedimentation, impacting composition and biomass of benthic and pelagic communities (Hop et al., 2023; Włodarska-Kowalczuk et al., 2019). These suspended particles can also impact the efficacy of eDNA capture. Fragments of eDNA can bind to suspended particulate matter and result in increased levels of DNA in a sample and even help reduce DNA degradation (Alvarez et al., 1998). However, turbid waters typical contain higher levels of PCR-inhibitors such as humic acids, which are extracted from filters along with the target DNA. The presence of these inhibitors can significantly hamper PCR amplification success and therefor eDNA sequencing results from water samples (Albers et al., 2013). The highest rates of melting are during the summer months, but particulate matter is also present during the polar night and the overall input is increasing in Arctic fjords with winter warming.

Kongsfjorden is the location of multiple long-term observation systems (Berge et al., 2020b) with the research station based in Ny-Ålesund and as a result, it is one of the best studied fjords in the Arctic. Despite intensive monitoring in the fjord over the last decades, however, studies on polar night biology are still comparatively low in number to the polar day. Thus, our main objectives were to implement eDNA metabarcoding to (i) conduct a survey of the eukaryotic community present during the polar night, (ii) combine eDNA with net-caught specimens to determine the gelatinous zooplankton community in detail and (iii) test for the impact if PCR-inhibitors on eDNA diversity recovered from turbid water of an Arctic glacial fjord.

2. Materials and methods

2.1. Sampling area

Sampling occurred in vicinity of the German-French Research station AWIPEV, located in Ny-Ålesund, KF, Svalbard, between January 20th – February 4th’ 2022. Kongsfjorden is on the western side of the island of Spitsbergen and is approximately 20 km long, 4–10 km wide and is located at approximately 79° N. There are five major tidal glaciers which terminate in the inner part of the fjord (Fig. 1). The polar night in KF takes place between 25th October and 17th of February (Berge et al.,

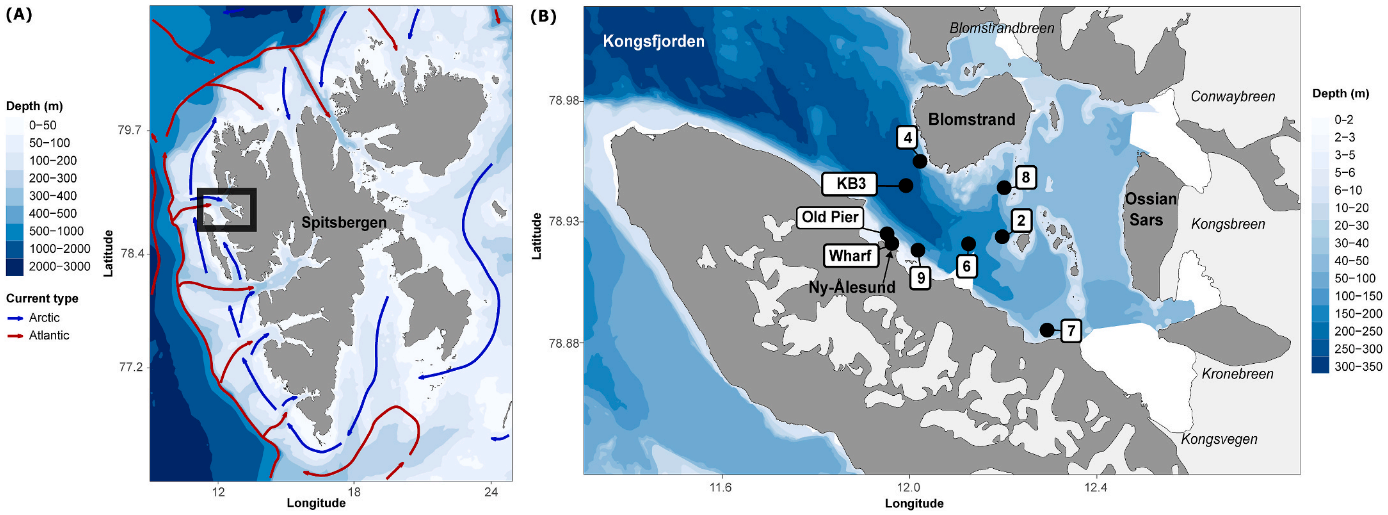

Fig. 1. Sampling Location. (A) Map of the Svalbard archipelago with the major Arctic and Atlantic currents. Sampling area is indicated by black polygon. (B) Map of sampling stations in Kongsfjorden. Black dots indicate the approximate location of the individual stations. Glacier names are indicated in italic text. Maps were produced using PlotSvalbard package in R: https://github.com/MikkoVihtakari/PlotSvalbard.

2015b).

2.2. Sampling

All samples were collected aboard the working vessel *Teisten* or from the pontoon attached to the wharf inside the harbour of Ny-Ålesund. All stations are located in the middle part of the fjord as sampling the outer and inner parts were limited by weather and ice conditions (Table 1 and Fig. 1).

2.2.1. Environmental data

Hydrographic profiles were conducted at each station (except the wharf) immediately before collecting water samples. Salinity and temperature data were measured using a MiniSTD conductivity-temperature-depth (CTD, SD-204, SAIV A/S, Bergen, Norway) sensor mounted in on a winch cable from the ship. Density plots were produced using the R package PlotSvalbard (Vihtakari, 2020) and the command *ts_plot*. The dominant water masses affecting KF are defined here as: Atlantic Water (AW, >3.0 °C and >34.65 psμ), Arctic Water (ArW −1.5 °C - 1.0 °C, 34.30–34.80 psμ), Intermediate Water (IW, >1.0 °C and >34.0–34.65 psμ) and Transformed Atlantic Water (TAW, >1.0 °C–3.0 °C and >34.65 psu) (Cottier et al., 2005). The distance of each station from land was calculated based on geodesic distances using the *dist2land()* function.

2.2.2. Gelatinous zooplankton net sampling

A WP3 net with a mesh size of 500 μm was deployed vertically from the working vessel at each station following completion of water eDNA sampling. The hand-net specimens were all caught in the inner harbour at from the wharf. All specimens were identified to the highest possible taxonomic resolution in the onsite lab using identification guides (e.g., Bouillon et al., 2006; Licandro et al., 2017; Licandro and Lindsay, 2017). Tissue for DNA extraction was aliquoted and either extracted immediately at the on-site lab or frozen at −80 °C for extraction at a later date in the home lab.

2.2.3. eDNA sampling

Seawater for eDNA metabarcoding was collected using Niskin bottles (Hydrobios, Kiel), which were either handheld (Wharf station) or deployed on a winch cable aboard the research vessel R/V Tiesten (all other stations). All stations were sampled once, except the 'Wharf' station, which was sampled three times on three different days. A total of 6L of water per sample was collected at each depth before being decanted into sterilized Kautex cannisters and stored below 0 °C until filtration (within a maximum of 6 h). Water was filtered across 0.22 μm Sterivex-GP filters (Merck Millipore) using a peristaltic pump and Masterflex tubing following Murray et al. (2024). Each 6L sample was split across three filters (up to 2 L on each filter) and the tubing was changed in between each sample. All sampling equipment and laboratory benches were sterilized with a solution of 1:10 bleach and milliQ wash, followed by a milliQ wash and dried using 70 % ethanol. A field

Table 1
Location and physical properties of sampling stations.

Station	Latitude	Longitude	Date sampled	Distance from land (km)	Water sample depths (m)	Sediment sample depth (m)
St. 2	78.93365	12.173167	20.01.2022	0.57	1, 10, 20, 30, 50, 70, AB	79
St. Old pier	78.932433	11.924717	27.01.2022	0.37	1, 10, 20, AB	36
St. 4	78.963183	11.9878	27.01.2022	0.44	1, 10, 20, 30, 50, AB	65
St. KB3	78.952833	11.960017	28.01.2022	1.56	1, 10, 20, 30, 50, 70, 100, 150, 200, 250, AB	–
St. 6	78.929983	12.10135	31.01.2022	1.74	1, 10, 20, 30, 50, 70, 100, AB	112
St. 7	78.895783	12.279233	31.01.2022	0.45	1, 10, AB	20
St. 8	78.954	12.172233	01.02.2022	0.50	1, 10, 20, 30, 50, AB	72
St 9	78.9263	11.992967	01.02.2022	0.50	1, 10, 20, 30, AB	70
St. Wharf_1	78.928533	11.936272	29.01.2022	0.03	1	–
St. Wharf_2			02.02.2022			
St. Wharf_3			04.02.2022			

Notes: AB refers to "Above Bottom, approximately 5–10 m of the sea floor. '-' indicates stations where no sediment was collected. Longitude and latitude are in decimal degrees. Wharf stations are at the same location and depth, but sampled on different days.

blank was collected for each station by filtering 1 L of milliQ water across a filter and was subsequently treated identically to all other samples. Filters where then stored at −80 °C for downstream processing.

Sediment for eDNA metabarcoding was collected using a Van Veen grab (KC Denmark, Silkeborg, Denmark) after seawater eDNA sampling at each station. The grab was opened at the top and the undisturbed upper layer of sediment (maximum 1 cm in thickness) was collected using a sterile spatula and stored in sterile 50 mL falcon tubes. The sediment was preserved at −20 °C for downstream processing. Disposable gloves were also used when processing all eDNA samples to avoid cross contamination between sampling sites.

2.3. *Molecular work*

2.3.1. *Tissue extraction and sanger sequencing of GZP specimens*

DNA was extracted from a total of 16 GZP individuals of 8 species, in order to confirm morphological identifications. The DNA of tissue from these individuals was extracted using the Qiagen Blood and Tissue kit (QIAGEN), following the manufacturer's protocol. DNA was eluted on 100 μL of elution buffer and stored at −20 °C until Polymerase chain reaction (PCR) processing. PCR amplification was conducted following the conditions in (Murray et al., 2023). The 'Folmer' fragment of the mitochondrial cytochrome *c* oxidase subunit 1 gene (COI) using the primer pair HCO 2198 (5′-TAAACTTCAGGGTGACCAAAAAATCA-3′) and LCO 1490 (5′-GGTCAACAAAT-CTAAAGATATTGG-3′) (Folmer et al., 1994). PCR product was sequenced bidirectionally by EUROFINS Germany. The resulting sequences were manually checked for spurious base calls and stop codons, primer sequences removed. The sequences and specimen data were submitted to BOLD where possible, and accession numbers are detailed in Table S1.

2.3.2. *eDNA extraction*

A total of 174 eDNA filters (165 samples and 9 field blanks) and 8 eDNA sediment samples were collected. Environmental DNA of the water samples was isolated from the filters using the Qiagen Blood and Tissue kit (QIAGEN) following (Murray et al., 2024). Extraction controls were made using a new Sterivex filter for each extraction event and processing it alongside the samples (9 in total). Sediment eDNA was extracted from a 10g subsample of vortex-homogenized sediment from each individual station. This was done using the Qiagen DNeasy PowerMax Soil kit according to the manufacturer's protocol. A total of 8 sediment samples and 1 extraction control were processed. DNA extractions and library preparation were conducted in separate, dedicated laboratory rooms and on different days to PCR and post-PCR steps. All equipment and benches were sterilized using a 10 % bleach solution followed by a milliQ wash and 70 % ethanol for drying, before being radiated with UV light for a minimum of 1 h before each extraction. During the extraction DNA-ExitusPlus™ (ITW Reagents) was used for sterilizing gloves and pipettes.

2.3.3. *PCR inhibitors-removal treatment on water samples*

Sediment was visible on the filter membranes after filtration of seawater for eDNA. In order to check for the significant negative effect of potential PCR inhibitors on sequencing, we processed and sequenced a small subset of the water eDNA samples (6 surface and 2 above bottom filters) with a post-extraction inhibitor removal kit. To do so, we treated 50uL of the DNA extract with the OneStep™ PCR Inhibitor Removal Kit from Zymo Research. The treated extracts were sequenced alongside the untreated extracts, resulting in 16 samples in total (8 treated and 8 with no treatment).

2.3.4. *Metabarcoding primers*

We used the universal eukaryote barcode of the mitochondrial DNA fragment known as the "Leray" fragment (Leray et al., 2013). It is an approximately 313-base pair region of the COI fragment that has been optimised to amplify eukaryotes. It has been successfully implemented in Arctic studies to investigate pelagic metazoan communities (Murray et al., 2024), coastal biodiversity (Lacoursière-Roussel et al., 2018; Leduc et al., 2019) and fjord benthic biodiversity (Mazurkiewicz et al., 2024). We used the highly degenerated Leray-XT primers pair: mICOIintF-XT: (5 ′GGWACWRGWTGRACWITITAYCCYCC3′) (Wangensteen et al., 2018) and the reverse jgHCO2198: (5′TAIACYTCIGGRTGICCRAARAAYCA3′) (Geller et al., 2013).

2.3.5. *Metabarcoding library preparation and sequencing*

For the inhibitor test, library preparation and sequencing were done by AllGenetics (Spain) following the same 2 step-PCR protocol as described in Murray et al. (2024). This dataset was also sequenced on the Illumina Novaseq 6000 platform and had four PCR controls. For the main water eDNA dataset, PCR was performed in triplicate, each with an individual PCR control. Sample-specific tags and a variable number of leading Ns (2–4) were attached to both the forward and reverse primers (tagged). The PCR master mix contained 10 μL of Amplitaq Gold Master Mix (Applied Biosystems), 0.16 μL of 20 μg/μL BSA, 5.84 μL molecular grade water, 1 μL each of 5 μM forward and reverse primers and 2 μL of DNA template. The PCR conditions were: denaturing for 10 min at 95^0C, followed by 35 cycles of 1 min at 94 °C, 1 min at 45 °C, 1 min at 72 °C, and a final extension for 5 min at 72 °C. PCR product was checked for successful amplification on 1.5 % agarose gel. PCR triplicates were then pooled at equal volumes before being purified with Min-Elute columns (Qiagen) and following the manufacturer's protocol before being pooled into a single library. The library pool was sent to Novogene (Cambridge, UK) for ligation of Illumina adaptors and sequencing on the Illumina Novaseq 6000 platform in a paired-end sequencing run.

2.4. *Bioinformatic analysis and curation of metabarcoding data*

The bioinformatic workflow was based on OBITOOLS 3 (Boyer et al., 2016), following Antich González et al. (2022) with some modifications (https://github.com/adriantich/MJOLNIR3). Briefly, libraries and samples of the main dataset were demultiplexed and the tags and primers removed using *ngsfilter*. The inhibitor dataset was demultiplexed by the sequencing company using *cutadapt* (Martin, 2011). OBITools 3 was used to merge paired-end reads, length filter and dereplicate sequences per sample. Chimaeric sequences were removed with the *uchime denovo* algorithm in VSEARCH *v2.28.1*. Sequences were denoised using *DnoisE v1.4* (Antich González et al., 2022) (alpha = 4) and a blank correction of 10 % was applied following Antich et al. (2021). Singletons were removed and a relative threshold abundance of 0.002 % for in each sample was applied to filter out sequencing artefacts. Next, denoised sequences were clustered into molecular operational taxonomic units (MOTUs) (d = 13) with SWARM *v3.1.5* (Mahé et al., 2021). Any remaining MOTUs with a total read count of <5 were removed. The *ecotaq* algorithm was used for taxonomic assignment against a custom reference database (https://github.com/adriantich/NJORDR-MJOLNIR3), which is comprised of reference sequences from GenBank, BOLD and in-house sequences. The post-clustering filter LULU *v1.0* (Frøslev et al., 2017) was used to remove potentially further erroneous sequences. Finally, bacteria were removed and nuclear mitochondrial pseudogenes (NUMTs) filtered out. Taxonomic assignments were further checked using the BOLDigger2 software *v2.2.1* (Buchner and Leese, 2020) and the Barcode of Life Data System (BOLD) (Ratnasingham and Hebert, 2007). Taxonomic assignments were improved and extra taxonomic information added where possible. The following identity thresholds were used: species (97 %), genus (95 %), family (90 %), class (85 %), phylum (80 %) following Murray et al. (2024). All MOTUs with taxonomic assignments <75 % were removed from the metabarcoding datasets completely.

The species-level detection lists were compiled from detections in all of the eDNA datasets combined. Detections in KF and Svalbard were based on Global Biodiversity Information Facility (GBIF) species occurrence data accessed via: https://www.gbif.org/species. When occurrences were not recorded on GBIF for KF or Svalbard, further literature searches were conducted and citations included in species tables where necessary.

2.5. Statistical analysis

Data visualisations and analyses were all done using R 4.3.0 using several R packages. Plots were made using *phyloseq v 1.46.0* (McMurdie and Holmes, 2013), *Fantaxtic v 0.2.0* (Teunisse, 2022), *microViz v 0.12.1* (Barnett et al., 2021) and *ggplot2 v 3.5.0* (Wickham, 2016) packages, and statistical analyses conducted with *vegan v 2.6.4* (Oksanen et al., 2019).

The main dataset was used for all community composition and beta diversity visualisations and analyses. Filter triplicates were pooled into single samples (one for each sampling depth at each station) by summing reads. The net-caught specimen data was only used for gelatinous zooplankton detections (presence-only). Due to different library preparation methods, number of PCR replicates and sequencing companies, the inhibitor test dataset was not combined with or compared to the main dataset. It was used only for testing the effect of a PCR inhibitor removal treatment on the DNA extract as well as in the presence-only list of genus and species detections. Relative read abundances were used to visualize the taxonomic composition. Alpha diversity indices (observed richness and Shannon-Wiener index) were used in the inhibitor treatment dataset. These were calculated based on read counts normalised using the Scaled Ranked Sums (SRS) method (Beule and Karlovsky, 2020) following Murray et al. (2024). ANOVA tests and subsequent pairwise comparisons were conducted to test for the effect of station, depth and inhibitor treatment on alpha diversity.

Spatial variance in community composition at the species level (main dataset only) were analysed through non-metric multi-dimensional scaling (NMDS) based on Aitchison's distances (centre log ratio transformation and Euclidian distance) to account for the compositional nature of metabarcoding data (Quinn et al., 2018). This was done to test for the effect of station, depth, inhibitor treatment and eDNA sample type (water or sediment) on beta diversity. PERMANOVA tests were used to check for significance between grouping factors using the *adonis2()* function, and beta dispersion was tested for using the *betadisper()* functions in *vegan*.

3. Results

3.1. Environmental conditions

Station KB3 was the deepest station sampled, with a bottom depth of approximately 300 m and the shallowest was the Wharf station with a bottom depth of approximately 4 m (Table 1). Distance of stations from land ranged from 0.03 km (Wharf) to 1.74 km (Station 6). Station KB3 was the closest to the fjord mouth and Station 7 closest to the glaciers (Fig. 1 and Table 1). The oceanographic conditions in winter 2022 did not vary greatly between sampling sites, with gradients occurring mostly with depth. Seawater temperatures ranged from −0.9 to 1.5 °C and salinity from 34.4 to 34.8 psu. Surface water temperatures were all below 0.5 °C and the warmest temperatures were measured below 50 m at Station 2 and KB3 (Fig. S1). Arctic water masses (ArW) were by far the most dominant with some Transformed Atlantic Water (TAW) measured at Station KB3 and Station 2, as a small amount of Intermediate Water (IW) measured at Station 2 (Fig. S2).

3.2. Sequencing results of main dataset

We sequenced a total of 164 samples, as well as 23 field blanks and laboratory controls. Two samples (one water and one sediment) and one extraction control (sediment) failed in sequencing and were removed from the dataset. The failed extraction control was checked for DNA concentration using a Qubit and contained no detectable DNA. A further three water filters were excluded from the dataset as outliers due to a small number of over dominant MOTUs. After data curation and blank correction, 161 samples remained (154 water filters and 7 sediment samples), with a total of 1,452,732 reads assigned to 1387 MOTUs. The sequencing depth per sample ranged from 8,325 to 101,768 and the mean number of reads was 24,622 reads per sample. Rarefaction curves plateaued or where approaching plateau for the majority of samples (Fig. S3), suggesting sequencing depth was sufficient to capture most of the diversity present. Separate MOTU accumulation curves for water and sediment samples plateaued for water samples, but not for all of the sediment samples. This suggests that more samples are needed to capture all of the diversity in the sediment. Approximately one third of the MOTUs assigned to domain only (Eukaryota). This was followed by assignments to kingdom level (64 %), phylum (54 %), class (34 %), order (23 %), family (17 %), genus (14 %) and species (12 %).

3.2.1. Community composition in water versus sediment eDNA

Relative read abundances of the eukaryotic groups varied between stations and sample types (Fig. 2A and B). The kingdom metazoan was more dominant in the water than the sediment samples. The kingdom Fungi was only detected in water, and the kingdoms Chromista and Plantae were more dominant in sediment samples compared to water. The variation between relative read abundance at the sampling stations, and the variation in the proportion of unassigned sequences, was higher in the sediment than the water samples.

A PERMANOVA revealed that community composition varied significantly between eDNA sample types of water and sediment (Sample Type: $F_1 = 10.6$, $p = 0.001$). This was further supported in the NMDS ordination plot (Fig. 2C). When comparing the shared MOTUs (presence-only), 62 % were detected only in the water samples and 10 % in the sediment. A total of 28 % of the MOTUs in the main dataset were detected in both water and sediment eDNA (Fig. 2D).

3.2.2. Water eDNA

The final water eDNA dataset (main dataset only) consisted of 1,222,037 reads assigned to 1250 MOTUs from 52 samples (filters triplicates combined). The primary producer component of the water samples was made up 119,993 reads assigned to 216 MOTUs. A total of 57 % these reads were assigned to Chromista and 43 % to Plantae. The most dominate primary producer phylum was Chlorophyta (40 % of primary producer reads in water and 13 MOTUs), followed by Dinoflagellata (31 % and 19 MOTUs), Ochrophyta (16 % and 66 MOTUs) and the remaining phyla (<5 %). We were able to detect a number of species in Chlorophyta, Ochrophyta and Rhodophyta, but the assignments were restricted to mostly class or order level in the other phyla (Fig. 3A). MOTUs assigned to the prasinophyte *Bathycoccus prasinos* made up 33 % of the primary producer reads, followed by MOTUs assigned to the dinoflagellate class Dinophyceae (15 %) and then MOTUs assigned only as Phaeophyceae (Phylum: Ochrophyta) with 12 %. The most dominant group at all stations were Chlorophytes, except for stations 7 and 8 where dinoflagellates were more dominant (Fig. 3A). MOTUs assigned to Heterokontophyta and Rhodophyta were present in low abundances at all stations, with the exception of station wharf, where there were significantly more reads assigned to Heterokontophyta.

A total of 947,392 reads were assigned to 559 metazoan MOTUs in the water samples. The most dominant metazoan phyla in both reads and MOTU richness were Annelida with 66 % of reads in the water and 145 MOTUs, followed by Arthropoda (22 % and 131 MOTUs). The next most abundant in reads were Echinodermata (4 % of reads and 15 MOTUs), Cnidaria (4 % of reads and 77 MOTUs) and then Chordata (1 % of reads and 31 MOTUs). The most abundant metazoan taxa were MOTUs assigned only to Annelida (63 %), followed by the copepod species *Microcalanus pusilis* (15 %) and the sea urchin *Strongylocentrotus droebachiensis* (4 %) (Fig. 3B). MOTUs assigned only to Annelida were the most dominant group at all stations, except for the Wharf station, where the copepod *M. pusilus* made up the highest proportion of reads.

We tested for station and sampling depth as drivers of community

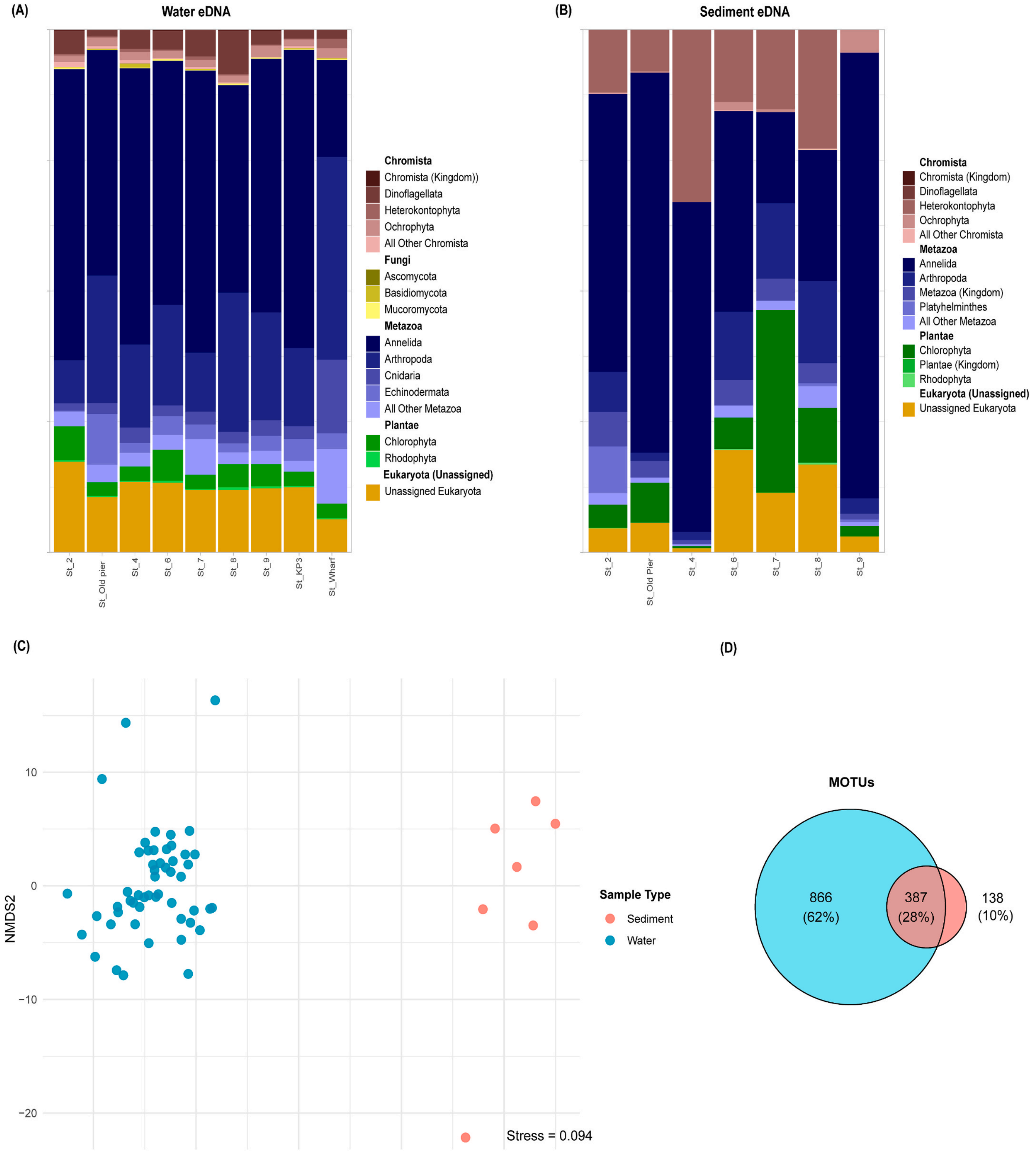

Fig. 2. Eukaryotic community composition in water and sediment eDNA samples. (A) Relative abundances of the top 4 phyla in each eukaryotic kingdom in water eDNA. (B) Relative abundances in sediment eDNA. (C) NMDS calculated using MOTUs agglomerated at species level assignments and Aitchison's distance. (D) Venn diagrams showing shared MOTUs and shared species between the sampling types. Venn diagrams are based on presence absence data only.

composition in the water eDNA. Only station had a significant effect on community composition (Station: $F = 3.4_8$, $p = 0.001$, $R^2 = 0.42$), and explained 42 % of the variation. This was supported by the clusters on the NMDS plot, where the majority of the stations form distinct clusters from one another, with the wharf being the most dissimilar to the other stations (Fig. 3C). This was further evidenced in the relative read abundances of the top 10 most abundant MOTUs at each sampling point (Fig. 3D). The wharf samples in particular were the most dissimilar to the other clusters (Fig. 3C), which is driven by higher proportions of *M. pusilis* reads than the other stations and relatively high proportions of

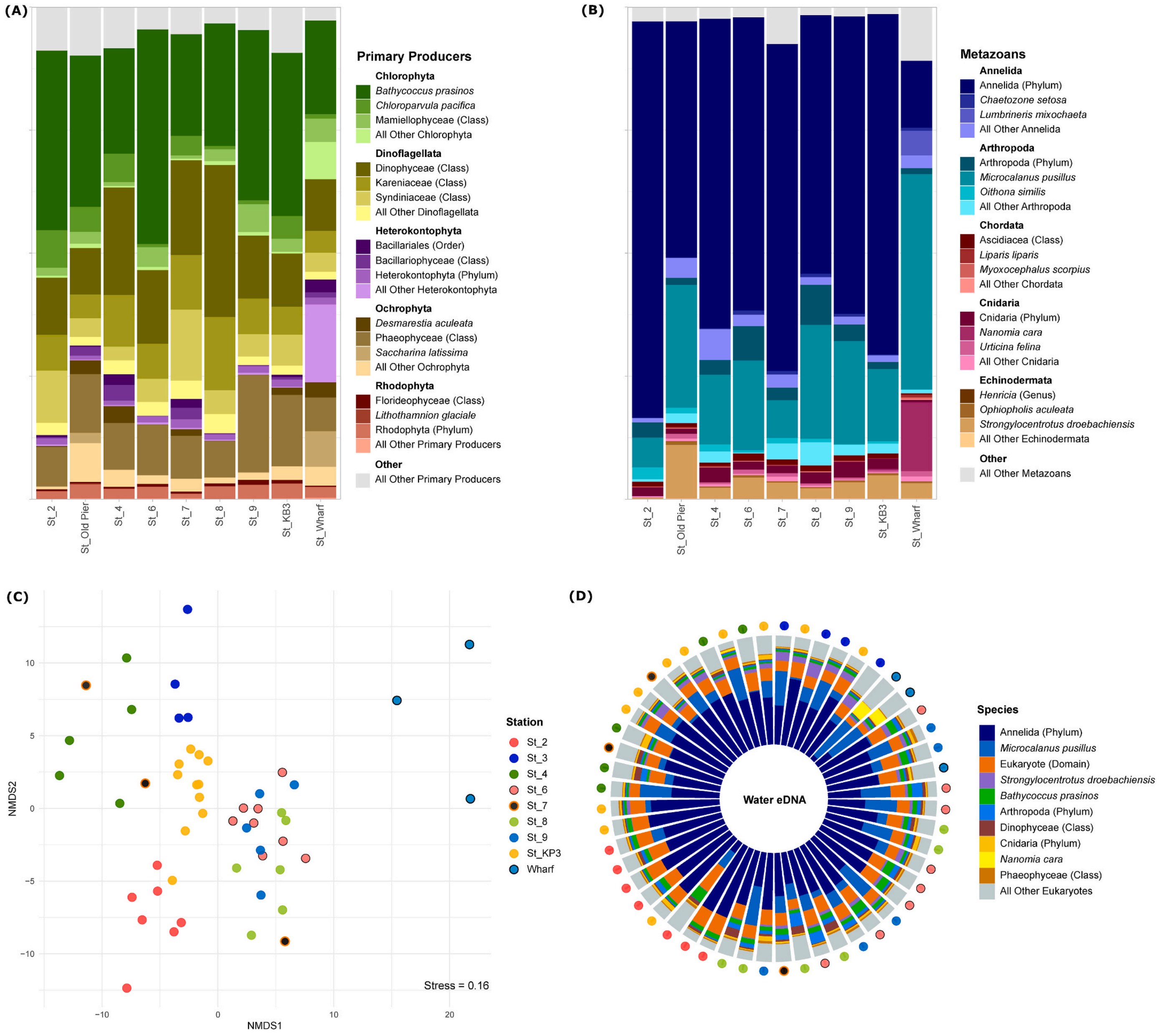

Fig. 3. Eukaryotic community composition in water eDNA. MOTUs are aggregated at species-level or the next highest taxonomic level possible. (A) Primary producers and (B) Metazoans. The five most abundant phyla and the three most abundant species in those phyla are shown. All other MOTUs are pooled together as “Other”. (C) NMDS plot of species composition based on CLR transformed and Euclidian (Aitchison’s distance) matrix of community composition. Colours indicate different depths (D) Iris plot of the RRA’s of the top 15 taxa at each sampling point. MOTUs are aggregated at species level where possible, and lower taxonomic levels when not. Each bar represents a sampling point. Bars are arranged in order according to the NMDS and the coloured circles next to each bar correspond to the stations on the NMDS plot. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

reads assigned of the siphonophore *Nanomia cara* (Fig. 3D). However, significant differences in beta dispersion for the grouping factor “station” were found. This is likely due to the uneven sampling sizes at the different stations due to different maximum depth profiles at each station (4 m–300 m). As a result, the clustering of the stations in the NDMS must be interpreted with some caution.

3.2.3. *Sediment eDNA*

The sediment dataset consisted of 230,695 sequenced reads assigned to 523 eukaryotic MOTUs across 7 samples. After data curation, 135 MOTUs were assigned to the primary producer kingdoms Chromista (66 %) and Plantae (35 %), totalling 58,956 reads. The most dominant primary producer phyla were Heterokontophyta (54 % of primary producer reads in sediment and 58 MOTUs), Chlorophyta (33 % and 14 MOTUs) and Ochrophyta (11 % and 32 MOTUs). The majority of MOTUs in the phylum Heterokontophyta could only be assigned to class or order level and MOTUs assigned to the order Chaetocerotales was the most dominant group, making up 26 % of the primary producer reads in the sediment. MOTUs assigned to Chlorophyta (phylum level) made up 21 % of primary producer reads, followed by those assigned only to Mamiellophyceae (10 %). In Ochrophyta, reads assigned to the species *Pylaiella washingtoniensis* were the most dominant (5 % of primary producer reads), followed by *Halothrix lumbricalis* (2 %). Phylum Heterokontophyta dominated in read abundance at all stations except St. 7, where Chlorophyta were more abundant, and St. 9 where Ochrophyta dominated the reads. Dinoflagellata where present in low abundances at all stations and Rhodophyta at all stations except St. 4 (Fig. 4A).

A total of 225 MOTUs were assigned as metazoans in the sediment.

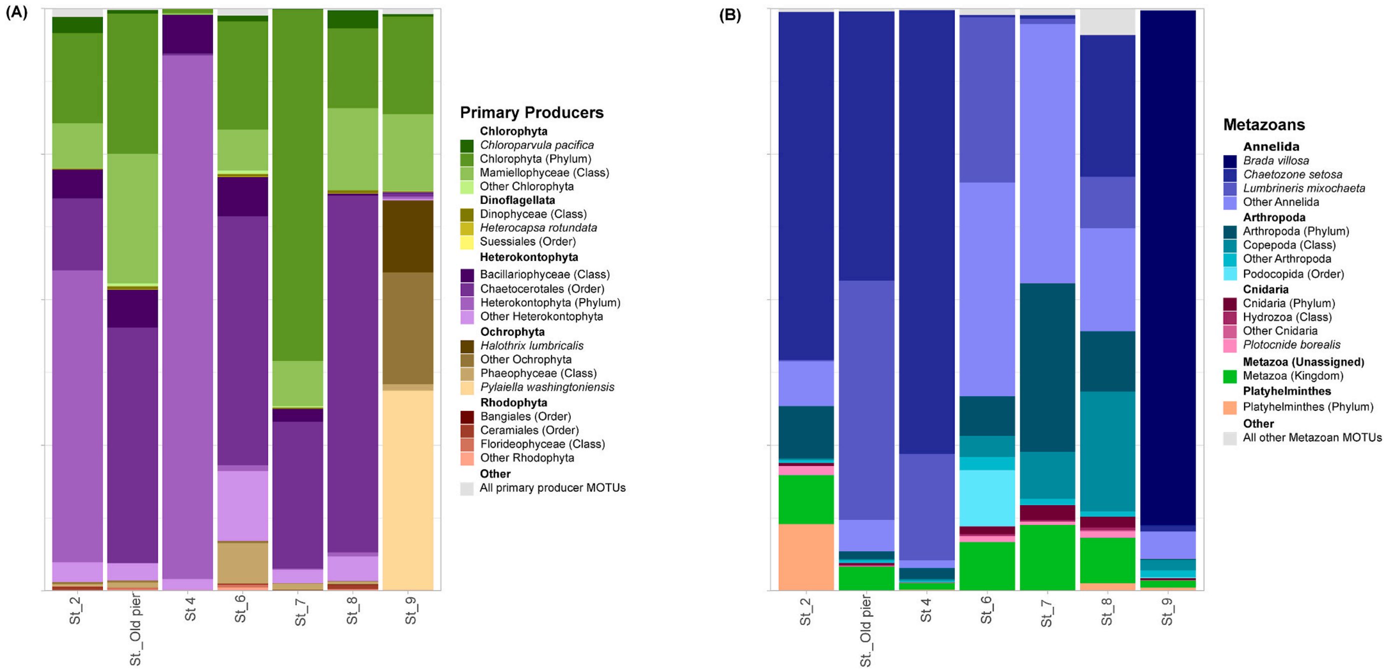

Fig. 4. Relative read abundances of most abundant primary producers and metazoans in the sediment eDNA. MOTUs are aggregated at species-level or the next highest taxonomic level possible. The five most abundant phyla and the three most abundant species in those phyla are shown. All other MOTUs are pooled together as "Other". (A) Primary producers and (B) Metazoans.

The most dominant metazoan phylum in both reads and MOTU richness was Annelida, which made up 73 % of metazoan reads in the sediment and was represented by 51 MOTUs. MOTUs assigned as the species *Chaetozone setosa* were the most abundant Annelida taxa (30 % of sediment reads), followed by *Lumbreineris mixochaeta* (14 %) and *Brada villosa* (13 %). The next most abundant metazoan phylum was Arthropoda (16 % of sediment metazoan reads and 59 MOTUs) and then Cnidaria (2 % and 32 MOTUs). In terms of reads number, Annelida were dominant phyla at all stations, but Arthropoda also made up a significant proportion of reads at stations 6, 7 and 8 (Fig. 4B).

3.3. PCR-inhibitor treatment dataset

Particulate matter was visible on the water filters after filtration due to suspended matter in the water, so a subset of 8 samples were treated and sequenced before the main data set to investigate the potential presence of PCR inhibitors (Kumar et al., 2022). After bioinformatic filtering and data curation, all samples were retained (8 treated and 8 untreated) with a total of 1,411,255 reads (>75 % identity match) assigned to 1275 MOTUs. Rarefaction curves plateaued for all samples, indicating that the sequencing depth was sufficient to capture the biodiversity in the samples.

We tested for the effect of inhibitor removal treatment on MOTU richness, Shannon diversity and total read counts. Richness and Shannon diversity were calculated based on SRS transformed values, and raw data was used for the read counts (Table S2). One-way ANOVA tests found that treatment did not have a significant effect on any of the values (Table S3). Analysis of community composition between the treated and non-treated samples showed no significant difference (PERMANOVA, $F_1 = 0.270$, $p = 0.885$). This indicates that inhibitor removal treatment did not have a significant effect on the beta diversity captured in sequencing. This was further supported by an NMDS ordination, which showed no obvious clustering between the treated and non-treated samples (Fig. S4).

3.4. List of species-level detections using eDNA metabarcoding

We were able to detect a total of 225 individual species using DNA metabarcoding of water and sediment samples. The highest number of metazoan species-level detections were in the phylum Annelida, with 65 assignments. This was followed by Arthropoda (30), Chordata (29) and Cnidaria (23) and then the remaining metazoan phyla. In the primary producers, the most species-level detections were found in the Chromista phylum Ochrophyta (22). This was followed by the Plantae phyla Rhodophyta (7) and Chlorophyta (4). The full list of species detections can be found in Table S4.

3.4.1. Macroalgae

We detected 29 species of macroalgae in the eDNA sampling. These included kelps (e.g., *Laminaria digitata* and *Saccharina latissima)*, filamentous brown (e.g., *Desmarestia aculeata*) and red algae (e.g., *Savoiea arctica*), as well as crusting red algae (*Lithothamnion glaciale* and *Boreolithothamnion lemoineae*). All of the species were found in water, and approximately half were found in both water and sediment. In total, five species were not previously reported in KF, four were new records in Svalbard and four were first molecular detections (Table 2).

3.4.2. Cnidaria

A total of 23 species-level assignments were recovered in the phylum Cnidaria, across three classes (Anthozoa, Hydrozoa and Scyphozoa). We detected sea anemones (e.g., *Urticina felina*), soft corals (e.g., *Gersemia rubiformis*), hydroids (e.g., *Calycella syringa*), siphonophores (e.g., *Nanomia cara*) hydromedusae (e.g., *Ptycogena lactea*) and large scyphomedusae (e.g., *Periphylla Periphylla*). All of the cnidarians were found in water eDNA, except for one (*Catablema vesicarium*) which was only found in the sediment. Three were found in both water and sediment samples. All of the anthozoans have been previously detected in Svalbard, and one of them in KF. A total of 6 of the hydrozoans have previously been found in KF, 11 in Svalbard and two more further south in Bear Island waters. A total 11 of the hydrozoan sequences we recovered were new detections for KF. Both of the scyphozoans have been observed previously in KF (Table 3).

Table 2
Species-level detections of macroalgae from eDNA samples.

Phylum	Class		eDNA type	Previously detected in KF	Previously detected in SV
Ochrophyta	Phaeophyceae	*Alaria esculenta*	W + S	Y	Y
		Chaetopteris plumosa	W	Y	Y
		Chorda filum	W	Y	Y
		Chordaria chordaeformis	W	Y	Y
		Chordaria flagelliformis	W + S	Y	Y
		Desmarestia aculeata	W + S	Y	Y
		Dictyosiphon ekmanii	W + S	**N**	**N**
		Dictyosiphon foeniculaceus	W + S	Y (Fredriksen et al., 2019)	Y
		Dictyosiphon sinicola	W + S	Y (Düsedau et al., unpublished results)	Y (Düsedau et al., unpublished results)
		Eudesme borealis	W	Y (Düsedau et al., unpublished results)	Y (Düsedau et al., unpublished results)
		Fucus distichus	W	Y	Y
		Halothrix lumbricalis	W + S	Y (Düsedau et al., unpublished results)	Y (Düsedau et al., unpublished results))
		Haplospora globosa	W + S	Y	Y
		Hedophyllum nigripes	W + S	Y (Dankworth et al., 2020)	Y (Dankworth et al., 2020)
		Laminaria digitata	W	Y	Y
		Laminariocolax aecidioides	W + S	Y[a] (Fredriksen et al., 2019)	Y (Fredriksen et al., 2019)
		Phaeosaccion collinsii	W + S	**N**	Y
		Pogotrichum filiforme	W	Y	Y
		Pylaiella washingtoniensis	W + S	Y (Düsedau et al., unpublished results)	Y (Düsedau et al., unpublished results)
		Saccharina latissima	W + S	Y	Y
		Saundersella doloresiae	W + S	**N**	**N**
		Stictyosiphon tortilis	W + S	Y[a]	Y
Rhodophyta	Phaeothamniophyceae	*Grania efflorescens*	W	Y[a] (Fredriksen et al., 2019)	Y (Fredriksen et al., 2019)
	Florideophyceae	*Ahnfeltia borealis*	W	**N**	**N**
		Boreolithothamnion lemoineae	W	**N**	**N**
		Devaleraea ramentacea	W + S	Y	Y
		Lithothamnion glaciale	W	Y[a]	Y
		Rhodomela lycopodioides	W	Y	Y
		Savoiea arctica	W	Y	Y

Note: W = water eDNA, W + S = water and Sediment eDNA, S = Sediment.
Previous detections based on observations listed in GBIF https://www.gbif.org/occurrence/search?occurrence_status=present&q = .
[a] present study is first molecular detection. Bold text indicates that the present study is the first record.

3.4.3. Arthropoda

We recovered 29 species-level assignments in the Phylum Arthropoda. These included five classes, with Malacostraca having the highest species richness. We detected species belonging to several crustacean groups including krill (e.g., *Thysanoessa longicaudata*), pelagic copepods (e.g., *Calanus finmarchicus*), decapods including shrimps (e.g., *Lebbeus polaris*) and crabs (e.g., *Hyas araneus*), amphipods (e.g., *Caprella septentrionalis*) and barnacles (e.g., *Semibalanus balanoides*). All of the Arthropoda species were found in water samples, and two were also found in sediment. All of the species have been found in Svalbard waters before except for two (the amphipod *Lembos websteri* and the euphausiid *Hansarsia megalops*). A further five have no previous detections in KF according to GBIF (Table 4).

3.4.4. Chordata

We recovered 23 species of vertebrates in the eDNA dataset, across three classes (*Aves, Mammalia* and *Teleostei*). These species included sea birds (e.g., *Cepphus grille*), sperm whale (*Physeter macrocephalus*), walrus (*Odobenus rosmarus*), seals (e.g., *Pagophilus groenlandicus*) and fish (e.g., *Mallotus villosus*). All vertebrate species-level detections were in water samples and none were found in sediment samples. All of these species have previously been recorded in Svalbard, and all but five in KF (Table 5).

3.5. Gelatinous zooplankton

We detected 19 gelatinous zooplankton to species-level and a further three to genus-level, with both net and eDNA sampling methods combined (Fig. 5). Of these, 15 were detected in water eDNA, three in sediment and 11 with nets. Of the net specimens, eight were confirmed with barcoding of the COI Folmer fragment. A total of 8 detections were unique to water eDNA, 1 to sediment eDNA and 6 to the nets. There were 5 species detected by both water eDNA and nets, but no overlaps between sediment and nets, nor all three methods. The dominant Arctic cnidarian (Hydrozoa and Scyphozoa) and ctenophore classes (Nuda and Tentaculata) were all detected. *Cyanea capillata* and *Nanomia cara* were ubiquitous across the water eDNA stations, while *Plotocnide borealis* was the most widespread in the sediment. In the nets, *Aglantha digitale, Sminthea arctica* and *Beroe* spp were the most widespread (Fig. 5).

4. Discussion

This study, to our knowledge, represents the first COI-based eDNA metabarcoding survey targeting Arctic marine eukaryotic biodiversity during the polar night. We successfully recovered a wide range of taxa belonging to the pelagic community, seabird, fish and mammals, as well as benthic and hyperbenthic taxa known to the area. Additionally, we detected species that were, based on existing literature and published datasets, previously not known to occur in the fjord or in the Svalbard area. Furthermore, by implementing a comprehensive sampling program targeting gelatinous zooplankton (GZP), we were able to provide a baseline dataset for a hitherto overlooked component of the winter pelagic community. Our study provides a baseline for future polar night eDNA-based biodiversity monitoring in Kongsfjorden (KF), a time of year that remains underrepresented in a highly-studied area of the Arctic.

4.1. Different eDNA assemblages recovered from water and sediment

Sample type-dependent eDNA assemblages have been well documented in marine systems (Cordier et al., 2022; Holman et al., 2019). Based on presence data alone, more than two thirds of the MOTUs detected here in the sediment were also present in the water samples (Fig. 2D). Yet multivariate analysis (Fig. 2C), which was based on transformed read abundance data, showed a significant difference in community composition between the two. This incongruence can be explained by many of the shared MOTUs being low in abundance in one of the two sample types, and the fact that more than double the amount

Table 3
Species-level detections in the Phylum Cnidaria from eDNA samples.

Phylum	Class		eDNA type	Previously detected in (KF)	Previously detected in Svalbard
Cnidaria	Anthozoa	*Gersemia rubiformis*	W	Y	Y
		Hormathia nodosa	W	**N**	Y
		Stomphia coccinea	W	**N**	Y
		Urticina felina	W + S	**N**	Y
	Hydrozoa	*Bougainvillia principis*	W	**N**	**N**
		Bougainvillia superciliaris	W	Y	Y
		Calycella syringa	W	**N**	Y
		Catablema vesicarium	S	**N**	**N**
		Lafoea dumosa	W	Y	Y
		Nanomia cara	W	Y	Y
		Obelia longissima	W	**N**	Y
		Opercularella lacerata	W	**N**	Y (Ronowicz et al., 2013)
		Orthopyxis integra	W	Y	Y
		Plotocnide borealis	W + S	Y	Y
		Ptychogena lactea	W	Y	Y
		Rathkea octopunctata	W	**N**	Y
		Sarsia lovenii	W + S	**N**	Y
		Sarsia princeps	W	**N**	Y
		Sarsia tubulosa	W	**N**	**N** (Bear Island)
		Stauridiosarsia producta	W	**N**	**N**
		Tiaropsis multicirrata	W	**N**	**N** (Bear Island)
	Scyphozoa	*Cyanea capillata*	W	Y	Y
		Periphylla periphylla	W	Y	Y

Note: W = water eDNA, W + S = water and Sediment eDNA, S = Sediment. Previous detections based on observations listed in GBIF https://www.gbif.org/occurrence/search?occurrence_status=present&q = .
Bold text indicates new detections.

of MOTUs were found in water versus sediment. Many benthic organisms release eDNA into the water column (e.g., gametes or excretion products), which could explain the presence of many of the sediment MOTUs in the water column. Indeed, previous research has found that benthic taxa left traces of eDNA in adjacent waters (Antich et al., 2021). Sediment also harbours eDNA of pelagic origin, but its persistence depends on many factors including but not limited to: microbial activity, taxon-specific decay-rates, DNA hydrolysis and temperature (reviewed in Torti et al., 2015). Hence, we would expect traces of the pelagic community in the sediment, and vice versa, but our findings further highlight the necessity of including multiple sample types when investigating both pelagic and benthic communities.

It must be noted that high levels of heterogeneity were observed between the sediment samples compared to the water samples (Fig. 2). In a previous Arctic coastal eDNA study Leduc et al. (2019) also found higher variation in benthic samples compared to pelagic samples. Sediment is a heterogeneous habitat that and can have significantly different assemblages from centimetres to kilometres (Angulo-Preckler et al., 2023; Hewitt et al., 2005; Nascimento et al., 2018). Indeed, KF has a range of benthic substrates (e.g., soft sediments and rocky shore), as well as ice-scouring and high glacier run-off, all of which are important drivers of benthic assemblages across relatively small spatial scales (Molis et al., 2019; Renaud et al., 2020). However, low sample numbers prevented statistical analysis of community composition between the sediment samples. The sediment also had lower total MOTU richness (523 MOTUs) than the water samples (main dataset: 1250 MOTUs, and inhibitor test dataset: 1275 MOTUs). This is contradictory to many other eDNA studies where sediment has typically higher richness than water-based eDNA (e.g., Cordier et al., 2022; Holman et al., 2019), but similar patterns have been detected before in aquatic studies (e.g., Sakata et al., 2020). The different levels of richness and between sample variation here may be explained in part by the differences in sampling strategies employed. The number of sediment samples was significantly lower than water samples (7 sediment and 52 water) and their sampling volumes differed (10g sediment vs 6L water per sample). Furthermore, the MOTU accumulation curves did not all reach asymptote for all of the sediment samples, indicating that increasing the sequencing depth is necessary to capture all MOTUs present in the samples. We used the extraction kit with the highest sample input volume of 10g (Pearman et al., 2020), which has been shown to more accurately reflect the community assemblages than other extraction kits with lower input volumes (Brinkmann et al., 2023). Thus, based on the rarefaction curves, low MOTU richness and the high between-site variation, we hypothesize that increasing the spatial resolution and number of sediment samples and sequencing depth rather than sample volume would be key to increasing the number of MOTUs, and therefore biodiversity recovered.

4.2. *Spatial patterns of community structure*

Contrary to other Arctic eDNA studies (Lacoursière-Roussel et al., 2018; Murray et al., 2024, 2025), we did not find a significant influence of depth on community composition in the water column. The polar night is the period with the highest levels of vertical mixing, as a result of wind and similar temperatures throughout the water column for example, compared to the coldest months of the year (Cottier and Porter, 2020; Tverberg et al., 2019). Thus, there is less stratification, which is also a general characteristic of the fjord in other seasons (except summer), resulting in a reduced vertical structuring. Further, the lack of sunlight prevents the accumulation of primary producers and associated higher trophic levels feeding on their production in surface waters. These factors likely result in high levels of localised dispersion of pelagic organisms and their eDNA signals throughout the water column, but to which extent cannot be determined based on the present study.

Multivariate analysis did, however, reveal that sampling location had a significant effect on pelagic community composition. The wharf, which was the shallowest station and experiences the most human disturbance (e.g., artificial light and vessel activity), showed the most dissimilar community composition compared to the other locations. However, the remainder of the stations were further out in the fjord and showed more similarity to one another (Fig. 3). Horizontal community structuring has been found before in coastal systems using water-derived eDNA (Jeunen et al., 2019; Lacoursière-Roussel et al., 2018), showing its potential to detect small-scale patterns despite possible dispersion. The relatively low levels of horizontal community structuring in the present study are likely influenced by the hydrological dynamics specific to the polar night, as well as tidal currents, eddies and advection events from the adjacent shelf via the West Spitsbergen Current (WSC) (Cottier et al., 2005; Tverberg et al., 2019), causing high connectivity between stations. Sampling location explained approximately 40 % of the variance in community composition here, suggesting further parameters should be measured to uncover other significant environmental factors. Furthermore, the extent of the sampling area was restricted to the central part of the fjord, omitting the inner fjord for example, where the influence of meltwater and sediment plumes from the tidal glaciers is stronger. Expanding the spatial range of sampling to encompass more of the fjord would likely increase the chance of uncovering distribution patterns and community structuring potentially overlooked in the

Table 4
Species-level detections in the Phylum Arthropoda from eDNA samples.

Phylum	class		eDNA type	Previously detected in Kongsfjorden (KF)	Previously detected in Svalbard
Arthropoda	Copepoda	*Tisbe furcata*	W	**N**	Y
	Malacostraca	*Lembos websteri*	W	**N**	**N**
		Calliopius laeviusculus	W + S	**N**	Y
		Caprella septentrionalis	W	Y	Y
		Gammarus locusta	W	**N**	Y
		Gammarus setosus	W	Y	Y
		Ischyrocerus anguipes	W	Y	Y
		Orchomenella minuta	W	Y	Y
		Pleustes glaber	W	Y	Y
		Anonyx sarsi	W	Y	Y
		Eualus gaimardii	W	Y	Y
		Lebbeus polaris	W	Y	Y
		Hyas araneus	W	Y	Y
		Pandalus borealis	W	Y	Y
		Hansarsia megalops	W	**N**	**N**
		Thysanoessa longicaudata	W	Y	Y
	Maxillopoda	*Calanus finmarchicus*	W	Y	Y
		Calanus hyperboreus	W	Y	Y
		Microcalanus pusillus	W + S	Y	Y
		Pseudocalanus acuspes	W	Y	Y
		Pseudocalanus minutus	W	Y	Y
		Pseudocalanus moultoni	W	**N**	Y
		Metridia longa	W	Y	Y
		Metridia lucens	W	Y	Y
		Oithona atlantica	W	Y	Y
		Oithona similis	W	Y	Y
		Triconia borealis	W	Y	Y
	Thecostraca	*Balanus balanus*	W	Y	Y
		Semibalanus balanoides	W	**N**	Y

Note: W = water eDNA, W + S = water and Sediment eDNA, S = Sediment.
Previous detections based on observations listed in GBIF https://www.gbif.org/occurrence/search?occurrence_status=present&q = .
Bold text indicates new detections.

Table 5
Species-level detections of Vertebrates.

Phylum	Class		eDNA type	Previously detected in Kongsfjorden (KF)	Previously detected in Svalbard
Chordata	Aves	*Cepphus grille* (Black Guillemot)	W	Y	Y
		Fulmarus glacialis (Fulmar)	W	Y	Y
	Mammalia	*Physeter macrocephalus* (Sperm Whale)	W	Y (Pöyhönen et al., 2024)	Y
		Odobenus rosmarus (Walrus)	W	Y	Y
		Erignathus barbatus (Atlantic Bearded Seal)	W	Y	Y
		Pagophilus groenlandicus (Harp Seal)	W	Y	Y
		Phoca vitulina (Harbour Seal)	W	Y	Y
	Teleostei	*Boreogadus saida* (Polar cod)	W	Y	Y
		Mallotus villosus (Capelin)	W	Y	Y
		Anarhichas lupus (Atlantic Wolffish)	W	Y	Y
		Gymnocanthus tricuspis (Arctic Staghorn Sculpin)	W	Y	Y
		Myoxocephalus Scorpius (Arctic Sculpin)	W	Y	Y
		Cyclopterus lumpus (Hen Fish)	W	Y	Y
		Liparis bathyarcticus (Nebulous Snailfish)	W	Y	Y
		Liparis fabricii (Gelatinous Snailfish)	W	Y	Y
		Liparis liparis (Sea Snail)	W	Y	Y
		Leptoclinus maculatus (Daubed Shanny)	W	Y	Y
		Lumpenus lampretaeformis (Serpent Blenny)	W	Y	Y
		Lycodes squamiventer (Scalebelly Eelpout)	W	**N**	Y
		Hippoglossoides platessoides (American Plaice)	W	Y	Y
		Hippoglossus hippoglossus (Atlantic Halibut)	W	**N**	Y
		Salvelinus alpinus (Arctic Char)	W	**N**	Y
		Ammodytes marinus (Launce)	W	**N**	Y

Note: W = water eDNA, W + S = water and Sediment eDNA, S = Sediment.
Previous detections based on observations listed in GBIF https://www.gbif.org/occurrence/search?occurrence_status=present&q = .
Bold text indicates new detections.

present study.

4.3. Primary producers

The phytoplankton community during the polar night in KF is characterised by low biomass during the winter months, but with a species occurrences similar to other seasons (Hegseth et al., 2019; Z. Smola pers. comm). In the present study, eDNA metabarcoding recovered a community composition largely congruent with the few studies that have targeted phytoplankton in the fjord. For example, the typical spring bloom genera *Micromonas* and *Phaeocystis* were found to be widespread in the water column of a neighbouring fjord during the polar

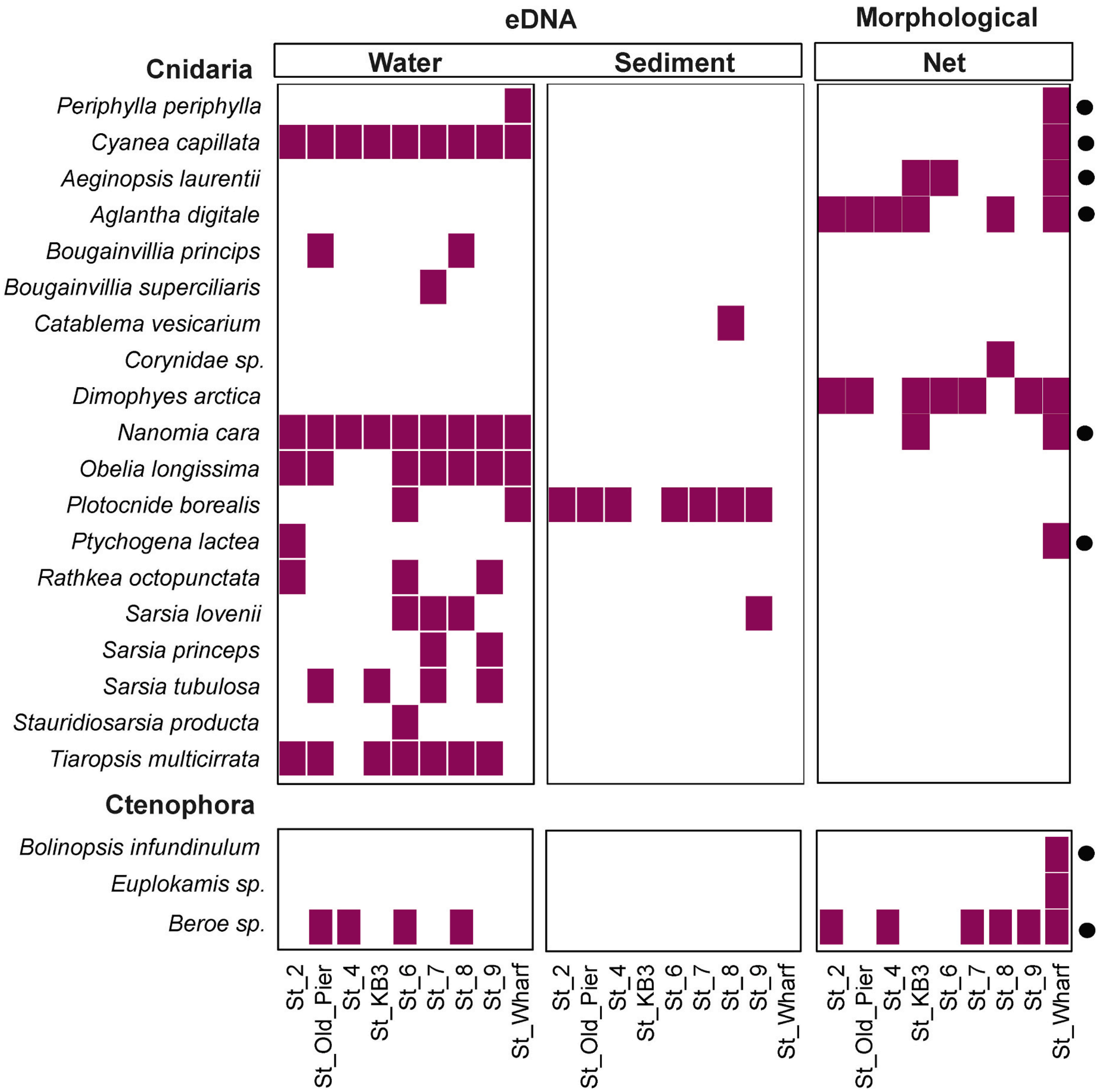

Fig. 5. Gelatinous zooplankton genus and species level detections in eDNA samples and nets. Presence of GZP at the different stations detected by the different sampling methods. Species detected in the main water eDNA and inhibitor test datasets are combined here under "water". Hand net and WP3 net caught specimens are combined under "Nets". Black circle indicates species of which net-caught specimens been barcoded.

night with eRNA (Vader et al., 2015). In the present study, we recovered *Phaeocystis* in low read abundances in the water column at every station. We also found *Micromonas* to genus-level in very low read abundances, as well as MOTUs assigned to the class Mamiellophyceae (e.g., *Bathycoccus prasinos*) which were widespread and in relatively high read abundances. Furthermore, we detected other genera typical of the spring bloom such as *Nitzschia*, *Entomoneis, Attheya, Chaetoceros* and *Skeletonema* (von Quillfeldt, 2000).

Many phytoplankton species have adaptions for winter survival that include some form of dormancy. For example, many diatoms form highly silicified resting stages that settle on surface sediment, while other species maintain active cells that persist in the water column in low abundances throughout the winter. These individuals then seed the spring bloom when the light returns at the end of the polar night (Hegseth et al., 2019; Hoppe, 2022). In the present study, we were able to detect evidence of these different overwintering strategies by using both water and sediment-derived eDNA. The most abundant (by reads) primary producer group in the water column, however, were assigned to the phylum Chlorophyta, which includes species that do not form resting stages at all, and thus overwinter as active cells in the water column. Similar observations have been made in another Svalbard fjord (Isfjorden) during the same time of year (Marquardt et al., 2016; Vader et al., 2015). Additionally, the fraction of diatom (Bacillariophyceae) reads in the sediment was significant, where they are traditionally considered to overwinter. Congruently, the high read abundance of the order Chaetocerotales in the sediment is indicative of a pelagic bloom forming species *Chaetoceros gelidus,* which is known to form particularly many resting stages (Booth et al., 2002; Chamnansinp et al., 2013). However, diatoms also made up a noteworthy proportion of the Heterokontophyta reads in the water column, adding to building evidence that indicates some cells stay present in the water column throughout the winter (Hoppe, 2022; Kvernvik et al., 2018; Vader et al., 2015). Dinoflagellates are considered to be the dominant component of the winter protist community, partially due to their mixotrophic characteristics. Interestingly, in the present study they were less dominant (in reads) than previously reported compared to Chlorophyta for example, hinting to a possible sampling bias of traditional (light microscopy-based) studies that underestimate the relevance of the picoplanktonic component of the pelagic community (MacKeigan et al., 2022).

The red and brown macroalgae composition was largely in agreement with published data from KF (Düsedau et al., 2024; Fredriksen et al., 2014, 2019), and four previously unrecorded species were detected as well. Macroalgae MOTUs made up a significant proportion of the sequence reads and species richness recovered by eDNA metabarcoding of both the water and sediment. In total, 29 macroalgae were detected to species level, including kelps, filamentous red and browns, and encrusting red algae. Many of these are well known in the fjord (e.g., *Saccharina latissima* and *Laminaria digitata*), while others have only been found at genus level (e.g., *Saundersella doloresiae*), or have no previous distribution data recorded in the fjord (e.g., *Ahnfeltia borealis* and *Boreolithothamnion lemoineae*). Recent research on macroalgae in the Arctic and North-Atlantic using eDNA metabarcoding of the 18S gene demonstrated eDNA as a useful tool for not only identify species but also determine the fate of macroalgae matter in sediments (Ørberg et al., 2023). Here, we show that the COI gene can also recover many brown and red macroalgae Arctic species from water and sediments and could be used in conjunction with other markers (e.g., Ortega et al., 2019), to detect similar patterns in KF. It is worth noting, that the identification of macroalgae using molecular approaches is generally challenging, because of their complex evolutionary history no universal protocol can be applied and they are highly underrepresented in the reference databases (Ortega et al., 2019; Saunders and McDevit, 2012, 2013). Most biodiversity assessments of this group in KF were therefore purely based on morphology (Fredriksen et al., 2014, 2019; Hop et al., 2012) but a recent DNA barcode survey revealed many overlooked and wrongly identified species (Düsedau et al., unpublished results). Significant regime and distribution shifts of macroalgal communities in KF were documented over the last three decades as a result of the rapidly changing environmental conditions in the fjord (Düsedau et al., 2024). For example, the Arctic endemic kelp *Laminaria solidungula*, that used to be rare but present at the sampling site Hansneset (Bartsch et al., 2016; Hop et al., 2012) was neither detected in the latest biomass sampling (Düsedau et al., 2024) nor in our metabarcoding analysis. Both polar night and eDNA-based studies targeting Arctic macroalgae are scarce, and filling polar night data gaps on macroalgae is essential in understand these changes on a seasonal scale.

4.4. Marine metazoans

Kongsfjorden hosts a diverse metazoan community, for which many important biological processes occur during the polar night. Previous research have shown activities such as feeding in bentho-pelagic amphipods (Dischereit et al., 2024a) and fish (Berge et al., 2015a), spawning of benthic taxa and Arctic fish species (Geoffroy and Priou, 2020), as well as high growth rates in bivalves (Berge et al., 2015a) all occur during these dark months. In the present study, we were able to detect pelagic and benthic metazoan taxa across a wide range of phyla, functional groups and sizes including, zooplankton, benthic fauna, marine mammals and fish.

Earlier polar night studies have found that zooplankton communities are dominated in species richness by crustaceans, and in number and biomass by copepods in particular (Berge et al., 2020a). Small copepod species tend to be the most abundant (Berge et al., 2015a) as they do not migrate to deeper layers but stay active in surface water (Barth-Jensen et al., 2022), which was a pattern reflected in the relative read abundances in our study. *Microcalanus pusilis* was the second most abundant MOTU and the most abundant arthropod species in the water samples, followed by another small copepod species, *Oithona similis*. Both species were ubiquitous across the stations sampled (Fig. 4). Interestingly, reads assigned to Annelida (e.g., polychaete species *Chaetozone setosa* and *Lumbrineris mixochaeta*) were the most dominant at almost every depth and station in the water eDNA. They are typically dominant in benthic fjord communities on Svalbard (Pawłowska et al., 2011; Wlodarska-Kowalczuk and Pearson, 2004), as well as in the polar night in KF (Kędra et al., 2011). Many arctic polychaete species reproduce via pelagic larvae (Fetzer and Arntz, 2008), and the dominance of Annelida reads observed here in the water column could indicate a large reproductive event during the polar night and therefore the presence of their pelagic phases.

Benthic fauna communities are disproportionally less studied during the polar night than their pelagic counterparts (Berge et al., 2015b; Renaud et al., 2020). While some studies have indeed been conducted at this time of year, which include benthic metazoans (Berge et al., 2015a, 2015b; Pawłowska et al., 2011), many ecological knowledge gaps remain. We found that polychaetes were the most dominant in terms of reads and richness in our sediment samples (Fig. 4). This is in line with a previous morphological study in the fjord, where polychaetes dominated the shallow water benthic communities at the end of winter (Kędra et al., 2011). We also detected other key groups including anthozoans (e.g., *Urticina feline*), the abundant sea urchin *Strongylocentrotus droebachiensis* and benthic and bentho-pelagic amphipods (*Anonyx sarsi, Gammarus* spp*, Orchominella minuta*). Additionally, we recovered many hyperbenthic species, which are predominantly crustaceans that inhabit the water just above the seafloor and perform migration to the feed in pelagic parts of the water column (McGovern et al., 2018). These included the shrimp *Pandalous borealis* and *Lebbus polaris,* as well as the amphipod (or skeleton shrimp) *Caprella septemtrionalis* which have previously been observed in January (McGovern et al., 2018; Renaud et al., 2020). Although we cannot distinguish between different life stages of these invertebrates using eDNA metabarcoding, this dataset provides important information on the diversity, distribution and community composition in a previously overlooked period.

Another salient finding was the high number of vertebrate species that we were able to detect using the COI marker, rather than 12S which is commonly used in eDNA studies targeting these groups (e.g., Jensen et al., 2023; Marques et al., 2023; Westgaard et al., 2024). We recovered 16 species of fish, five marine mammals and two sea bird in the water samples, but no vertebrate MOTUs in the sediment. All of these species have previously been found in Svalbard waters and many in KF itself. Detection of marine mammals and seabirds is largely reliant of visual observations, while fish monitoring is reliant on trawls, all of which are hindered by the logistical challenges of sampling at this time of year (e.g., ice conditions and lack of daylight). Moreover, trawling can damage the benthos and be detrimental to the health of benthic communities (Jennings et al., 2001; Jørgensen et al., 2019). We demonstrate that eDNA has the potential to extend at least one kind of sampling to a year-round timeframe, as a means to monitor seasonal variations in marine communities in the fjord. Indeed, eDNA has already been successfully been combined with traditional sampling methods and human observations in other parts of the Arctic to increase the detection of both fish and marine mammals (Schiøtt et al., 2023; Westgaard et al., 2024). Furthermore, sequencing vertebrate-specific markers using the same eDNA extracts would no doubt increase the species missed by COI and allow for stronger conclusions to be drawn regarding their diversity and distribution.

4.5. Gelatinous zooplankton in the polar night

Understanding of gelatinous zooplankton ecology in the Arctic is limited, including in Svalbard fjords and especially during the polar night. Evidence of overwintering by large scyphozoans and ctenophores has been found in the Chukchi Sea (Purcell et al., 2018), yet studies on the European side of the Arctic are lacking. In the present study, we recovered a high richness of GZP species present in KF during this period, with 19 species-level detections and a further three to genus-level recovered by eDNA and plankton nets combined. Additionally, we detected many more cnidarian MOTUs, which could only be assigned with low taxonomic resolution due to gaps in reference databases, potentially including further GZP taxa. This is more than has been recovered previously in morphological zooplankton studies that included GZP in the summer. In a 20-year summer zooplankton monitoring study (1996–2016), using MultiNet, Tucker Trawl and MIK net sampling, Hop et al. (2019) found 10 genera and species to be regular inhabitants of KF. In a polar night zooplankton study, Grenvald et al. (2016), reported six species as well as unidentified appendicularians, but in low abundances compared to crustaceans. The hydrozoan *Aglantha digitale*, and the ctenophores *Mertensia ovum* and *Beroe cucumis* were reported to be the most abundant GZP in the summer surveys, and the polar night survey did not report abundance data for individual species but GZP as a group. We detected many of the same taxa in the present study, with the notable exceptions of the small hydrozoan *Sminthea arctica* and appendicularians. Juvenile ctenophores were caught in the nets, likely including *M. ovum,* but we were unable to identify to a high resolution morphologically or confirm with COI barcoding. One explanation for the lower species richness in previous studies in KF is the sampling biases associated with using traditional plankton nets and trawls to sample GZP (Hosia et al., 2017). The fragility of their gelatinous bodies means that they are often destroyed, discarded or identified with low taxonomic resolution and grouped as “GZP” or “other”. Many species also have life stages such as planula larvae or benthic polyps which are easily missed and lead to underestimates of richness and distribution. Overall, we recovered a GZP community richer than was previously found with morphological surveys during daylight months, and found many of the summertime GZP to be present during the polar night. Furthermore, the presence of juvenile ctenophores, which has also been observed in previous years (Berge et al., 2020a), suggests that reproduction regularly occurs during these dark months. However, without year-round monitoring that targets GZP, it is not possible to determine significant differences between the community present in the polar night and other periods. Nor is it currently possible to elucidate whether there has been a recent increase in GZP richness with ongoing Atlantification or whether the GZP diversity uncovered in the present study is typical of the fjord.

As expected, we recovered different GZP communities depending on the sampling strategy used (Fig. 5), with only five genera/species recovered by both molecular and morphological methods. This is in line with a previous GZP study in Fram Strait, which found that eDNA, nets and optical surveys had some overlaps but also many unique detections, depending on the sampling equipment used (Murray et al., 2024). Morphological studies still provide many benefits, including abundance estimates for less-easily destroyed species and providing tissue for barcoding. However, we demonstrate here that the use of eDNA metabarcoding increased the number of GZP species detected by morphological methods alone. Furthermore, using eDNA to supplement morphological methods enabled us to detect cnidarians, such as hydroids, that have medusae stages representing an otherwise overlooked component of the Arctic GZP community. In addition, by barcoding specimens caught in nets, we were able to confirm species identifications and provide regional-specific sequences to public reference databases, which can improve the accuracy of future eDNA detections. Overall, by combining both molecular and morphological sampling strategies, our understanding of the polar night GZP community in KF has increased significantly.

4.6. *eDNA detection in turbid fjord waters*

Biodiversity recovered from sampling eDNA in turbid waters can be negatively impacted by the presence of particulate organic matter and associated PCR-inhibitors. When filtering water-eDNA samples in the present study, we found visible sediment deposits on the filter membranes, indicating high levels of water turbidity during sampling. Common strategies for reducing the impact of PCR-inhibitors in environmental samples is to either remove them from the DNA extract using specific DNA extraction kits, use a post-extraction inhibitor removal kit (Kumar et al., 2022) or including bovine albumin serum (BSA) in the PCR master mix (Albers et al., 2013). Based on the statistical comparison between sequencing outputs of treated and non-treated samples in the present study, we found that using a post-extraction PCR-inhibitor removal kit had no significant impact on the alpha diversity indices nor beta diversity, indicating that it was not necessary to prevent PCR-inhibition despite high levels of water turbidity present. Our findings indicate that the inclusion of BSA was likely sufficient to safeguard against the impacts of potential PCR inhibitors associated with water turbidity. Indeed in certain circumstances water turbidity may have positive impacts on eDNA sampling. Previous studies have found that extracting eDNA from the suspended particles can actually result in high DNA yields, alluding to yet another eDNA-based strategy for biodiversity surveys (e.g., Díaz et al., 2020). Additionally, due to the binding of eDNA to suspended particulate matter, some studies have found significantly higher DNA yields in turbid marine waters compared to clear waters, and may require smaller sampling volumes as a result (Kumar et al., 2022).

4.7. *eDNA as a tool for polar night surveys*

Despite a relatively low number of environmental samples in the present study, we were able to detect many of the common eukaryotic groups and species that are known to inhabit KF and the surrounding area and detect new species to the fjord or even the entire archipelago. Morphological studies in the fjord typically involve specialized sampling methods which target specific groups (e.g., bentho-pelagic trawls for fish, pelagic net sampling for zooplankton, and benthic grabs for benthos), that can be difficult to deploy in the polar night due to low visibility, and dangerous weather and ice conditions. As highlighted in our integrated survey of GZP, eDNA is a valuable tool for complementing morphological methods, but it has its own drawbacks and biases which can lead to false negatives. One such issue is primer-related biases that mean even “universal” barcodes such as COI are unable to amplify some species (Wangensteen et al., 2018), and well-known gaps in public reference databases that can prevent high-resolution taxonomic identification in some taxa (Hestetun et al., 2020). Despite these limitations, eDNA-based surveys remain a highly valuable tool in the challenging conditions of the polar night, where light, wind and ice conditions often restrict other sampling possibilities. The addition of environmental RNA (eRNA) sampling to future eDNA surveys in KF would be a valuable addition to spatio-temporal analysis of the marine community, due to eRNA signals being exclusively produced by metabolically active organisms (Giroux et al., 2022; Pearman et al., 2020; Scriver et al., 2025).

5. Conclusion

Our findings highlight the potential of eDNA metabarcoding to produce a large amount of high-quality biodiversity data that encompasses different taxonomic and functional groups, from unicellular phytoplankton to large marine mammals, all from the same small volumes of water or sediment. The present study relied on a relatively limited sampling effort, yet recovered many taxa known to inhabit the fjord and produced species lists for major marine functional groups, all of which contribute valuable baseline data for the polar night period. Understanding the patterns of diversity, community composition and distribution of marine organisms in the polar night is essential for monitoring the impacts of global climate change on sensitive Arctic marine ecosystems. Future eDNA monitoring in KF during the polar night, and indeed year-round, could serve as a powerful tool for detecting more taxa as well as small-scale patterns with increased spatial coverage and frequency. Finally, including further environmental parameters and data such as weather events and fluorescence would allow for exploration into the drivers of diversity and community composition uncovered by eDNA metabarcoding.

CRediT authorship contribution statement

Ayla Murray: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Adria Antich:** Writing – review & editing, Software, Data curation. **Annkathrin Dischereit:** Writing – review & editing, Methodology, Investigation. **Luisa Düsedau:** Writing – review & editing, Writing – original draft, Data curation. **Clara J.M. Hoppe:** Writing – review & editing, Writing – original draft, Data curation. **Charlotte Havermans:** Writing – review & editing, Resources, Project administration, Investigation, Funding acquisition, Conceptualization.

Data availability statement

Net dataset is publicly available at: https://doi.org/10.1594/PANGAEA.955899.

The raw metabarcoding sequence data used in this project are publicly available at NCBI on the SRA database under the BioProject ID: PRJNA1306041.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107443.

Data availability

I have shared the data links in the maine document.

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