



Tracking biodiversity in changing Arctic waters: insights from eDNA metabarcoding in Svalbard

Martine J. van den Heuvel-Greve^{1,2} · Marcel Polling³ · G. Arjen de Groot³ · Linda Kodde³ · Ingeborg M. Mulder¹ · Hans Verdaat¹ · Paul E. Renaud^{4,5} · Audun Schrøder-Nielsen⁶ · Michal Torma⁶ · Hugo J. de Boer⁶ · Quentin Mauvisseau⁶

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Abstract

Monitoring biodiversity patterns and their changes in Arctic coastal ecosystems is critical under ongoing climate change. However, common current approaches require high effort and expertise and this in turn limits the spatial and temporal scale of these monitoring efforts. Here, we investigated both the fish and the marine invertebrate communities across Svalbard using a multi-marker environmental DNA metabarcoding approach. We collected and analysed marine water, sediment and zooplankton filtered from marine water from sites influenced by the warm West Spitsbergen Current and the cold East Spitsbergen Current. Following metabarcoding amplification using mitochondrial COI, 12S, 16S and nuclear 18S markers and high-throughput sequencing, we retrieved an extensive overview of Svalbard marine biodiversity. Water, sediment and especially zooplankton samples collected across Svalbard revealed spatial differences in community composition, with significantly distinct assemblages in the northwest and southeast of Svalbard. We identified potential bioindicator species for use in rapid assessment of impacts of marine temperature increase and confirmed observed patterns of ongoing shifts in community structure as a response to changes in dominant water masses. Overall, our findings show that species composition depending on fine-scale climate variation of Arctic waters can be effectively studied and monitored using environmental DNA. These insights can help us understand current and evolving climate-driven changes.

Keywords Biodiversity · eDNA · Metabarcoding · Svalbard · Climate variation

Introduction

Anthropogenic activities, primarily climate change, pollution, and habitat degradation, are inducing unprecedented changes in ecosystems worldwide (Scholze et al. 2006; Hoegh-Guldberg & Bruno 2010). Increased ocean acidification, temperature variability and atmospheric carbon dioxide concentrations are leading to reductions in species richness and ecological functions that impact every corner of the planet, leading to an ongoing event described as the sixth mass extinction (Barnosky et al. 2011; Ceballos et al. 2015). These environmental shifts are triggering cascading effects on trophic networks, nutrient cycling, and other ecosystem processes (Pace et al. 1999; Baum and Worm 2009; Rosenblatt and Schmitz 2016; Laws 2017).

Arctic systems have been warming at nearly four times the global average since 1979 (Rantanen et al. 2022). Rising Arctic oceanic temperatures are facilitating the northward movement of organisms previously constrained by low

✉ Martine J. van den Heuvel-Greve
martine.vandenheuvel-greve@wur.nl

✉ Quentin Mauvisseau
quentin.mauvisseau@nhm.uio.no

¹ Wageningen Marine Research, P.O. Box 77,
4400 AB Yerseke, The Netherlands

² Marine Animal Ecology, Wageningen University,
P.O. Box 338, 6700 AH Wageningen, the Netherlands

³ Wageningen Environmental Research, Wageningen UR,
P.O. Box 47, 6700 AA Wageningen, The Netherlands

⁴ Akvaplan-niva, Fram Centre, 9296 Tromsø, Norway

⁵ University Centre in Svalbard, P.O. Box 156,
9171 Longyearbyen, Svalbard, Norway

⁶ Natural History Museum, University of Oslo, 0562 Oslo,
Norway

temperatures (e.g., Osland et al. 2021). These biogeographical shifts have led to a phenomenon called Arctic Borealization, which is characterized by the northward migration of boreal species (Fossheim et al. 2015; Polyakov et al. 2020; Husson et al. 2024), with studies reporting the occurrence and establishment of new non-indigenous species (NIS) in Arctic areas due to newly available suitable habitats (Chan et al. 2019; van den Heuvel-Greve et al. 2021; Adeniran-Obey & Osagie 2024).

Arctic ecosystems are typically vulnerable to these northward movements of organisms (Callaghan & Jonasson 1995; Wassmann 2011; Gilg et al. 2012), and borealization will exacerbate existing challenges and further disturb ecosystems, especially when combined with pressures coming from local human activities such as the introduction of NIS and pathogens (Nentwig 2008; Vilà & Hulme 2017; Kahric et al. 2022). As a result, research on the impacts of climate change is recognized as a priority concern for the Arctic in general (Drinkwater et al. 2010; Luo et al. 2011; Ford et al. 2021), and its coastal regions in particular (Sejr et al. 2024).

To assess and mitigate the impacts of NIS and other human stressors on marine communities, reliable biomonitoring strategies are urgently needed (Danovaro et al. 2016; Babafemi et al. 2024; Thyrring et al. 2025). In remote and extreme Arctic environments, such as in Svalbard, extensive efforts have been conducted to monitor pollution (Norstrom et al. 1998; Warner et al. 2019; Andersson Stavridis et al. 2024). Structured marine biomonitoring, however, remains a challenge due to the limited access and infrastructure, as well as the associated high costs and logistic complexity of sampling, decreasing the establishment of larger-scale coastal monitoring programs (Sander et al. 2006; Medeiros et al. 2021; Sorokina 2022; Gluchowska et al. 2016; Walkusz et al. 2009; Weslawski et al. 2010). So far, data collection targeting Svalbard's marine ecosystems has relied on traditional sampling methods, including morphological identification of samples obtained by grabs, fishing, netting and/or trapping (Brand and Fischer 2016; Gluchowska et al. 2016; Weslawski et al. 2010). While well-established, these methods are costly, time consuming, invasive and associated with sampling biases (Gold et al. 2021; Capurso et al. 2023). Their deployment on a larger scale is limited and is often associated with false-negative results, especially for rare or alien species in the early stage of the invasion (Pottier et al. 2020; Van Helmond et al. 2020) or species that do not preserve well, such as jellyfish, using common preservation techniques (Hosia et al. 2017).

To address these challenges, the use of molecular-based detection methods has emerged as a promising and complementary tool for accurate detection of aquatic biodiversity

(Burian et al. 2021; van den Heuvel-Greve et al. 2021; Mauvisseau et al. 2022; Burian et al. 2023). Also called environmental DNA (eDNA) detection, this non-invasive approach relies on the detection of DNA traces left by living or dead organisms in the environment (Bohmann et al. 2014; Thomsen and Willerslev 2015; Mauvisseau et al. 2022). This monitoring method has been generally found to be accurate, more cost-effective and less labour-intensive than traditional monitoring tools, and reliable in its detection of species presence at very low abundance or in larval stages (Zaiko et al. 2018; Ershova et al. 2019; Mauvisseau et al. 2019b, a; Beng and Corlett 2020; Brys et al. 2020), as long as validated sequences are available in molecular databases. As a result, recent studies have started to explore the use of eDNA-based monitoring in Svalbard marine systems (van den Heuvel-Greve et al. 2021; Willassen et al. 2022; Marques et al. 2023; Geraldi et al. 2024; Murray et al. 2025). However, factors including but not limited to variations within the sampled media (i.e., freshwater or marine water, plankton, sediment, terrestrial and even airborne environments), sample preservation, metabarcoding primers used for eDNA amplification prior to sequencing, replication and sampling strategy can significantly affect the amplification and detection of the total species richness (Deiner et al. 2017; Ruppert et al. 2019; Mauvisseau et al. 2021; Anmarkrud et al. 2025). This can lead to large variation in biodiversity estimates and to an incomplete understanding of ecosystem processes, structure or functioning. Therefore, a clear understanding of the trade-offs associated with the sampled medium and metabarcoding primers used is needed to further assess whether and how eDNA-based monitoring can be considered a reliable tool to monitor biodiversity and further identify long-term ecological changes driven by global warming in the Arctic.

Here, we investigated the use of eDNA-based monitoring from different marine substrate matrices in Svalbard (marine water, marine sediment and plankton) in combination with various primer sets (targeting mitochondrial 12S, 16S, COI, and nuclear 18SV4, 18SV9 regions) for metabarcoding amplification and additionally performed taxonomic identification of several collected organisms. We aimed to investigate (i) the feasibility of eDNA-based biomonitoring across these substrates, (ii) potential trade-offs between sample types and primer sets to detect marine biodiversity, and (iii) effectiveness of eDNA metabarcoding in identifying differences in community structure along the Svalbard coast influenced by colder or warmer ocean currents. Finally, we aimed to (iv) identify potential indicator species that could be used as a proxy to assess community shifts as a result of global warming.

Material and methods

Study area

Ranging from 74° to 81° North (latitude) and 10° to 35° East (longitude), the Arctic Archipelago of Svalbard lies at the northwestern edge of the Barents Sea (Fig. 1). The archipelago is approximately 60% covered by glaciers and has a predominantly Arctic climate (König et al. 2014). Svalbard is influenced by two main currents: the relatively warmer West Spitsbergen Current (WSC) with Atlantic water running along the west side from south to north, and the East Spitsbergen Current (ESC), characterized by colder Arctic water and with lower salinity running along the east side of the archipelago and flowing to the southwest and around the southern tip of Svalbard moving north closely along the coast as the Sørkapp Current (Walczowski 2013; Descamps et al. 2017; Piskozub 2017)

(Fig. 1). A simplified overview of these currents can be found in Fig. 1, and additional information about these currents and their impacts can be found in (Nilsen et al. 2016) and (Strzelewicz et al. 2022).

Sample collection was performed in four main areas. In the northwest, influenced by the WSC, this was done in (i) Ny-Ålesund harbour in Kongsfjorden, (ii) Krossfjorden (EH-Ebeltoftthamna and FJ-Fjortende Julibukta), and (iii) Longyearbyen harbour in Adventfjorden. On the southeast side of Svalbard, influenced by the ESC, several locations were sampled in (iv) Storfjorden (KL-Kapp Lee, RD-Rosenbergdalen, SB-Sundbukta and RB-Russabukta). Additionally, Hornsund (HS) is located in the far southwest of Svalbard, and is mainly influenced by the cold Sørkapp Current. Two of the sample locations were located directly near human settlements (the harbours of Ny-Ålesund and Longyearbyen), whereas the others were referred to as ‘reference locations’, away from human settlements. We later refer to the areas impacted by the ESC as “cold”, to the areas impacted by the

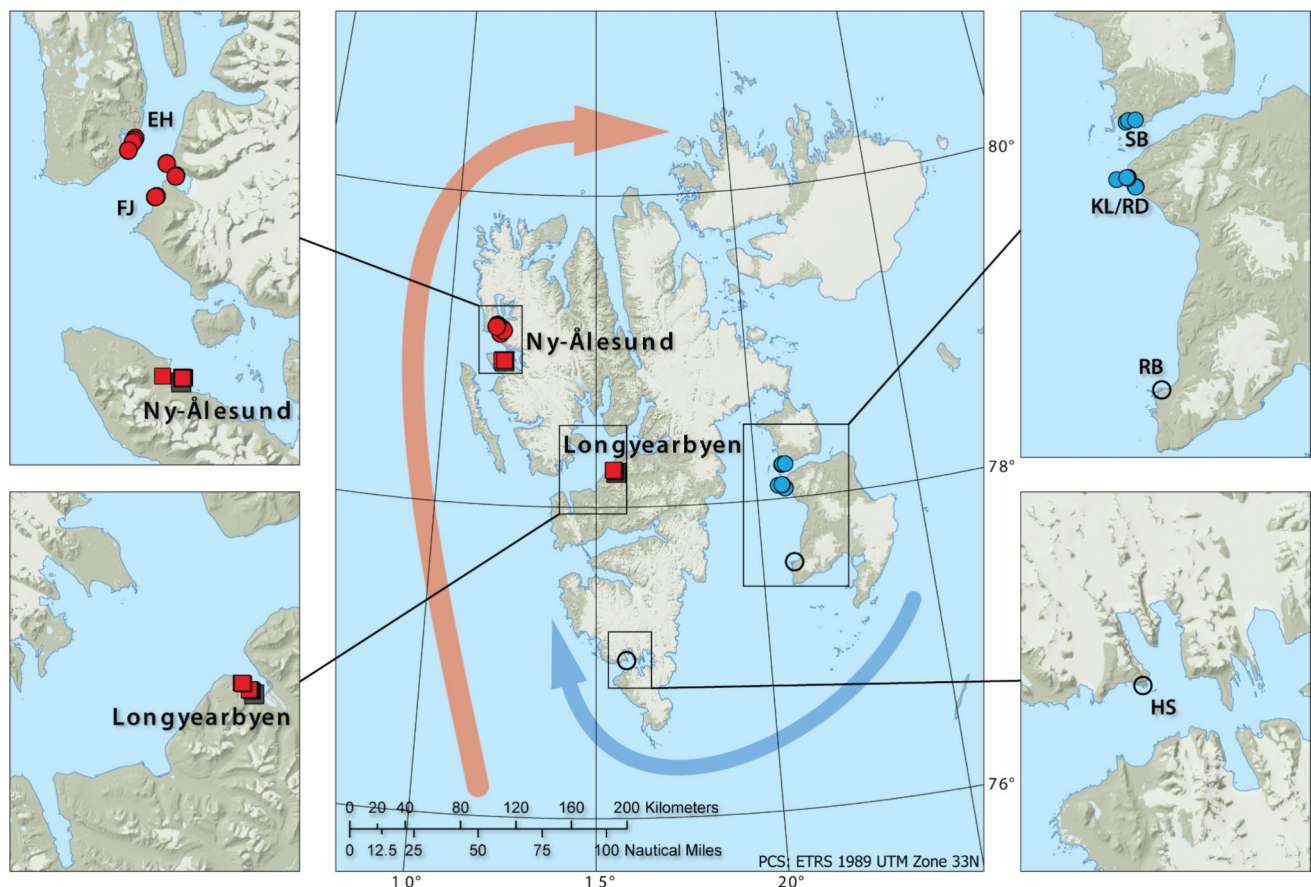


Fig. 1 Coastal locations around Svalbard were sampled in July–August 2022. Warmer west side: *EH* Ebeltoftthamna, *FJ* Fjortende Julibukta, *NA* harbour Ny-Ålesund, *LY* harbour Longyearbyen. Colder southeast: *SB* Sundbukta, *KL* Kapp Lee, *RD* Rosenbergdalen, *RB* Russabukta. Southwest sample location: *HS* Hornsund. A simplified illustration of the main currents is depicted by arrows: warmer Atlan-

tic West Spitsbergen Current (pink) and colder Arctic East Spitsbergen Current (light blue). Map by F. Steenhuisen, based on the Norwegian Polar Institute. Created by F. Steenhuisen, based on Kartdata Svalbard 1:100 000 (S100 Kartdata)/Map Data [Dataset]. Norwegian Polar Institute <https://doi.org/10.21334/NPOLAR.2014.645336C7>

WSC as “warmer”, and to areas under the influence of both ESC and WSC as “intermediate”.

Fieldwork and eDNA sampling

Fieldwork was conducted between July 13th and August 2nd, 2022, in separate expeditions to the southeast of Svalbard, to Ny-Ålesund research station, and in Longyearbyen (Fig. 1). The first consisted of the SEES.NL/2022 (Scientific Expedition Edgeøya Svalbard) expedition, a Dutch-led expedition to Edgeøya combining science with polar tourism (from 13th to 22nd July 2022; Lamers et al. (2024)). The second expedition was conducted from the Ny-Ålesund research station (25th July to 1st August 2022). Sampling in Longyearbyen harbour was conducted prior to, between, and after these two expeditions.

Water eDNA

A total of 63 water samples were collected for eDNA analysis (Table S1). For each sample, 2 L of water (collected approximately 10 cm under the water surface) was filtered on site using an eDNA Citizen Science Sampler device (Smith-Root, USA) and a 5.0 µm self-preserving filter unit (Smith-Root, USA). eDNA samples were then preserved dry and cool in the dark until further processing in the laboratory. Sterile equipment and disposable gloves were used at each location to avoid potential cross-contamination across sites and/or sampling methods. Field blanks were not performed due to logistical challenges associated with carrying large amounts of sterile water at the various sampling locations.

Sediment eDNA

In total, 43 eDNA samples were collected using a Van Veen grab sampler (Beukema 1974; van den Heuvel-Greve et al. 2021). At each site, one grab was taken from the seafloor and approximately 40 g of wet sediment was scraped from the top 2 cm of the collected sediment using a sterile metal spoon and stored in a sterile 50 mL falcon tube at −20 °C until further processing and DNA extraction in the laboratory.

Zooplankton

A total of 53 zooplankton samples were collected (Table S1) using a cleaned and rinsed plankton net from a vertical haul from just above the seafloor to the surface. Plankton concentrated in the cod end (i.e., terminal section of the net) was directly poured into a sterile 50 mL falcon tube and subsequently stored at −20 °C until further analysis.

Dedicated equipment was used for sediment and zooplankton sampling, and any reusable items were extensively

cleaned with a solution containing 10% bleach between each sampling location to prevent cross-site and collection method contamination. Despite these efforts, we acknowledge the potential for contamination from plankton nets and grab samplers.

Taxonomic analysis

Additionally, water, sediment and zooplankton samples were collected at a few reference locations (Storfjorden and for water and plankton also Krossfjorden) for visual taxonomic identification (see Table S2) to further validate the eDNA data. Finally, in both Longyearbyen and in Ny-Ålesund harbours, four settlement cubes (15 * 15 * 15 cm) were deployed for up to six weeks (June–late July 2022). After retrieval, fouling organisms were scraped from both the inner and outer parts of the cubes and collected and stored at −20 °C until further analysis (Tables S3–S5). Details regarding the preservation, taxonomic identification and analytical procedure of the collected organisms in each different media are provided in Table S2, Table S3, Table S4, Table S5.

DNA extraction and amplification

Water eDNA samples were extracted in a dedicated eDNA laboratory at Wageningen Environmental Research using the Environmental DNA isolation kit (Sylphium, Groningen, NL) following the manufacturer’s protocol. Sediment eDNA samples were extracted following the same protocol as used in van den Heuvel-Greve et al. (2021) using the DNeasy Powermax soil kit (Qiagen) with slight modifications from the manufacturer’s protocol. In brief, sediment samples were kept cool on ice and homogenised using an Ultra Turrax (T25) instrument equipped with an in-house constructed titanium dispersing shaft (Aylagas et al. 2016; van den Heuvel-Greve et al. 2021), and an 8 g subsample of the homogenised volume was extracted using the Powermax kit. Zooplankton samples were extracted using the DNeasy Blood and Tissue Kit (Qiagen, Hilden, DE) following the manufacturer’s protocol. For all sample types (water eDNA, sediment, zooplankton) we included negative extraction controls for each batch of 23 samples and included these in the sequencing run.

Metabarcoding was conducted using a multi-locus approach to increase biodiversity recovery across all sample types (e.g., Burian et al. 2023). All samples collected in this study (i.e., 43 sediment, 53 zooplankton and 63 water samples) were analysed using different primer sets (Table 1). All three sample types were amplified using the mICOIntF_v2 and jgHCO2198 primers (Leray et al. 2013; van den Heuvel-Greve et al. 2021) to target a 313-base-pair fragment of the mitochondrial Cytochrome Oxidase I (referred to later as

Table 1 Applied markers per sample type

Sample type	COI (Leray et al. 2013)	12S MiFish (Miya et al. 2015)	16S Fish (Nester et al. 2020)	18SV4 (Stoeck et al. 2010)	18SV9 (Amaral-Zettler et al. 2009)
Marine water eDNA (<i>n</i> =63)	✓	✓	✓		
Marine sediment eDNA (<i>n</i> =43)	✓				
Zooplankton (<i>n</i> =53)	✓			✓	✓

the COI primer set). The zooplankton samples were additionally amplified using nuclear 18S rRNA primers for both the 18SV9 subregion using primers Euk_1391f–EukB2 (approximately 100 to 150-base-pair amplified fragment) (Amaral-Zettler et al. 2009) as well as the 18SV4 subregion using primers TAREuk454FWD1–TAREukREV3_v1 (approximately 400 to 450-base-pair amplified fragment; Stoeck et al. (2010); van den Heuvel-Greve et al. (2021)). Finally, the water samples were amplified using the MiFish primer set (referred to later as 12S MiFish) targeting a variable ~160–180-base-pair fragment of the mitochondrial 12S rRNA gene (Miya et al. 2015), and the 16S primer set referred to from now on as 16S Fish (Nester et al. 2020), targeting a 200-base-pair fragment of the mitochondrial 16S rRNA gene. The 12S MiFish and 16S Fish primer sets were used to mainly target fish diversity. These barcode regions were used due to their short conserved targeted regions showing high amplification success across organisms and allowing an increased resolution during taxonomic assignment (Chen et al. 2025).

PCR amplification followed a two-step protocol to create dual index amplicon libraries. In the first round of PCRs, all primers were flanked by Fluidigm CS1/CS2 adapters at their 5' ends, and PCRs were performed in duplicate and later combined after amplification to account for stochasticity in the PCR reaction. Each reaction consisted of a 12.5 µL final volume including 1 U Platinum Taq (Fisher Scientific, Hampton, USA), 1×PCR buffer, 2.5 mM MgCl₂, 5% mM Trehalose, 200 ng/µL BSA, 200 µM dNTP, 250 µM water, 2 µL of 250 µM of each primer and 2.0 µL of sample DNA extract. The PCR programme consisted of a 2 min activation at 94 °C, followed by 15 cycles of 30 s denaturation at 94 °C and annealing for 3 min using a touchdown program starting at 56 °C and decreasing by 1 °C each cycle (touchdown PCR), 1 min elongation at 72 °C, followed by 20 cycles of 30 s at 94 °C, 3 min at 39 °C and 10 min final extension at 72 °C. In addition to the various eDNA samples, all negative extraction blanks, two PCR negative controls and one G-block positive control (COI: *Eupoecila australasiae*, an Australian scarab beetle known not to occur in Europe; 18SV4: *Swartschewskia papyracea*, a sponge species endemic to Lake Baikal; 18SV9: *Natatolana albinota*, an Antarctic isopod species) were included for each primer

combination. A mock community consisting of a known concentration of DNA extracted from Malagasy fish tissues (i.e., *Rheocles derhami*, *Oreochromis niloticus*, *Paretroplus maculatus* and *Awaous banana*) (Carvalho et al. 2024a, b) was also included in the PCR workflow of the COI primer set.

Following PCR amplification, the amplicons were sent to Genome Quebec (Canada) for further high-throughput sequencing, where a second PCR reaction was conducted to add sample-specific index barcodes and Illumina adapters (van den Heuvel-Greve et al. 2021). Indexed amplicons were then pooled per primer set and sequenced on an Illumina NovaSeq 2×250 bp paired-end, v3 kit (COI and 18SV9) or on a NovaSeq 2×150 bp PE (12S MiFish, 16S Fish and 18SV9) alongside eDNA samples from another project. Raw sequencing data following metabarcoding analysis are deposited on Zenodo <https://zenodo.org/records/16636529> and <https://zenodo.org/records/16639855>.

Bioinformatics and filtering

Raw fastq files were demultiplexed by Genome Quebec, who provided R1 and R2 files for each sample. All files were renamed into the QIIME2 format and imported into the QIIME2 platform version 2023.2 (Bolyen et al. 2019). The “cutadapt” plugin (Martin 2011) was used to delete forward and reverse primers from both the R1 and R2 sequences, using a minimum sequence length of 200 base pairs (COI, 18SV4) or 70 base pairs (12S MiFish, 16S Fish and 18SV9) and a maximum error rate of 0.2, discarding any reads that were untrimmed. The sequences were subsequently joined and denoised into ASVs (Amplicon Sequence Variants) and chimeras were removed using the DADA2 plugin (Callahan et al. 2016). Following visual inspection, the forward and reverse reads for COI and 18SV9 were truncated during this step at 200 base pairs (COI) or 90 base pairs (12S MiFish, 16S Fish and 18SV9), while no read truncation was applied for 18SV4 due to the large length variation at this locus (Callahan et al. 2016). After this step, for COI only ASVs with a length of 3 base pairs shorter or longer than the expected 313 base pairs amplicon size were kept, and the resulting ASVs were clustered using VSEARCH into 98% clusters (OTUs; Operational Taxonomic Units) to reduce the number of

sequences with identical taxonomic identifications (Rognes et al. 2016). Since we did not know the barcoding gap for the 18S, 12S MiFish and 16S Fish markers, we did not cluster these ASVs into OTUs. Finally, to determine whether a sequence represented an actual biological sequence or a potential sequencing or PCR error, the LULU algorithm was used applying the standard settings (Frøslev et al. 2017).

For COI, taxonomy assignment was performed using the BOLDigger package version 2.1.1 (Buchner and Leese 2020) that makes it possible to access all records on the Barcode Of Life Data (BOLD) system, including early access and private records. The option “digger_hit” from the JAMP pipeline was used to obtain the last common ancestor of the top 20 hits returned from the BOLD website and all flagged hits were manually curated (<https://github.com/VascoElbrecht/JAMP>, Elbrecht et al. 2018). The following thresholds were used: at least 98% sequence similarity for species level identification, 95% for genus, 90% for family and anything lower was classified to the order level. 12S MiFish, 16S Fish, 18SV9 and 18SV4 sequences were classified using a BLASTn search against the NCBI GenBank nt database (downloaded 03–2024). All sequences were curated using a lowest common ancestor (LCA) approach, requiring at least 95% query coverage and 97% identity match, and collapsing to the LCA if the percentage identity between consecutive hits differed by less than 0.5% (Mousavi-Derazmahalleh et al. 2021). The resulting identifications were manually checked for correctness in terms of geography using information from GBIF and the Ocean Biodiversity Information System (obis.org).

Following bioinformatics processing, all sequences for all markers were filtered using the following steps: all unassigned and non-target identifications were removed, including Archaea, Bacteria, Fungi and Viridiplantae since the selected primers are not optimised for these groups. All sequences with fewer than 10 reads across all combined samples for each OTU (for COI primers) and ASV (for 12S MiFish, 16S Fish, 18SV4 and 18SV9 primer sets) were removed from the dataset. If an OTU/ASV had more reads in any of the negative controls than in any of the samples, it was removed from the dataset. For COI, 18SV4, 18SV9 and 16S Fish no taxa were lost during this process, as only unassigned sequences were removed. For 12S MiFish, three fish species were removed as they were only detected in the negative controls: *Alburnus alburnus*, *Phoxinus* sp. and *Barbatula barbatula*. Subsequently, the maximum read count of any sequence in a negative control was subtracted from all samples. Then, the maximum number of reads from the positive control or mock community in any of the other samples was used as a filtering threshold to correct for potential leakage. This resulted in filtering out identifications that did not exceed 0.001% of the total sum of reads per OTU/ASV. The OTUs/ASVs with identical taxa identification were merged before further statistical analysis. For each

sample, only OTUs/ASVs representing more than 0.1% of the total reads were retained for downstream analyses, following the recommendations of Clarke et al. (2017) for zooplankton metabarcoding. For uniformity in our dataset, we subsequently used this filtering step for all other markers too.

Statistical analyses

Statistical analyses, as well as data manipulation and visualisation were performed using R version 4.2.1 (R Core Team 2020). We compared the community retrieved using the COI primer set and three sample types (i.e., eDNA from water, eDNA from sediment and plankton samples). Jaccard (presence/absence) and Bray–Curtis (relative read abundance) dissimilarity indices were calculated between all sample pairs using the *vegdist* function in the *vegan* package in R (Oksanen et al. 2018), as well as Aitchison distances. The corresponding values were ordinated using NMDS and visualised using the *ordiplot* function in *vegan*, grouped per sampling location. Statistical significance was tested using a permutational multivariate analysis of variance (perMANOVA) with 999 permutations, using the *adonis2* function in *vegan*.

Species distribution maps

Species distribution maps were generated from GBIF occurrence data (<https://github.com/gbif-norway/svalbard-species-map/tree/main>) for two marine species in the Svalbard region (10°E–35°E, 74°N–81°N) (Fig. S1, Fig. S2). The dataset comprised 77,536 records from 155 datasets, filtered for coordinate uncertainty ≤ 20 km and absence of geospatial issues. Maps were created using a 20 km $\times$ 20 km grid system with occurrence counts aggregated per cell. Distribution patterns were visualised using a colour gradient from orange (low density) to dark red (high density), with legends showing actual occurrence numbers. Maps were generated using Cartopy and Matplotlib in Python, with Lambert Conformal Conic projection centred at 20°E, 77.5°N. The GBIF occurrences can be found here (<https://www.gbif.org/occurrence/download/0005649-260120142942310>) and the code used to generate the maps can be accessed here (<https://github.com/gbif-norway/svalbard-species-map/tree/main>).

Results

DNA metabarcoding

A total of 106.1 M raw reads were obtained following metabarcoding amplification and sequencing using the COI primer set, divided as follows: 15.3 M reads for the sediment samples (on average 355 k $\pm$ 391 k reads per sample), 29.4 M reads for the water samples

(452 k $\pm$ 300 k per sample) and 61.4 M reads for the zooplankton samples (1.1 M $\pm$ 401 k reads per sample). For the 18SV4 primer set, 47.6 M reads were obtained for the zooplankton samples (mean sequencing depth of 897 k $\pm$ 184 k reads per sample) while 28.7 M reads were obtained for the 18SV9 primer set, consisting of 15.7 M reads for the zooplankton samples (on average 296 k reads $\pm$ 70 k reads per sample) and 13 M reads for the water samples (324 k $\pm$ 83 k reads per sample), 17.4 M for the 12S MiFish primer set used for water samples (245 k $\pm$ 123 k reads per sample), 14 M to the 16S Fish primer set (197 k $\pm$ 144 k reads per sample). Following bioinformatics processing, quality filtering, data cleaning based on positive and negative controls, per-sample OTU/ASV removal of 0.1% and removal of OTUs/ASVs assigned to Archaea, Bacteria, Fungi and Viridiplantae, we ended up with a total of 87.7 M assigned to the COI primer set (538 k reads $\pm$ 501 k SD per sample), 47.3 M to the 18SV4 primer set (893 k $\pm$ 184 k reads per sample), 15.6 M to the 18SV9 primer set (294 k $\pm$ 70 k reads per sample), 17.4 M to the 12S MiFish primer set (245 k $\pm$ 123 k reads per sample), 14 M to the 16S Fish primer set (197 k $\pm$ 144 k reads per sample). The OTU/ASV tables for each primer set following processing and data cleaning, as well as Venn diagrams displaying the number of species identified using the various primer sets can be found in (<https://zenodo.org/records/18319004>).

A total of 177 unique species were detected across the 63 sites where marine eDNA surface water samples were collected. Overall, 22 fish species were detected using the 12S MiFish primers, and the same number was found for the 16S Fish primers. The list of detected fish species using eDNA water samples is provided in Table S7. Using the COI primers, we detected 134 taxa. When combining the detection results of the 12S MiFish and 16S Fish primers using presence/absence detection (Fig. 2A) and relative read abundance of water samples (Fig. S3A), we found significant differences in the marine fish community composition ($F=2.59$, $R^2=0.31$, $p<0.001$, stress=0.24) and relative read abundance ($F=8.97$, $R^2=0.54$, $p<0.001$, stress=0.22) among the different locations investigated despite relatively low R^2 values. When analysing marine eDNA water samples using COI primers with presence/absence results, we found that the marine community composition differed across the sites distributed amongst cold, intermediate and warm locations ($F=5.36$, $R^2=0.40$, $p<0.001$, stress=0.18) (Fig. 2B). This was also the case when using relative read abundance ($F=5.35$, $R^2=0.40$, $p<0.001$, stress=0.20) (Fig. S3B). However, it should be noted that the stress levels of the NDMS in Figs. 2A and Fig. S3A make the interpretation of the results difficult and that these values indicate complex relationships between the different communities.

A total of 181 unique species were detected using the COI primer set across the 43 sites where sediment eDNA samples were collected. We found significant differences in the community composition ($F=4.12$, $R^2=0.25$, $p<0.001$, stress=0.18) (Fig. 3) and relative read abundance ($F=3.60$, $R^2=0.25$, $p<0.001$, stress=0.19) (Fig. S4) between locations characterised by different hydrographic conditions. Although NMDS ordination showed substantial overlap among locations, this likely reflects projection of high-dimensional differences into two dimensions rather than absence of compositional differences. Again, it should be underlined that the stress levels of the NMDS make the interpretation of the results difficult and that these values indicate complex relationships between the different communities.

Finally, a total of 1574 unique species were detected across the 53 sites where zooplankton samples were collected. Of these, 853 species were detected using the 18SV4 primer set, 982 species using the 18SV9 primer set, and 82 species using the COI primer set. Using the 18SV4 primer set, we found significant differences in the community composition based on presence/absence ($F=4.40$, $R^2=0.36$, $p<0.001$, stress=0.19) (Fig. 4A) and based on relative read abundance ($F=8.97$, $R^2=0.54$, $p<0.001$, stress=0.18) (Fig. S5A), among the different locations investigated. Similar observations were achieved using the 18SV9 primer set, in both the community composition ($F=4.79$, $R^2=0.39$, $p<0.001$, stress=0.19) (Fig. 4B) and relative read abundance ($F=8.50$, $R^2=0.53$, $p<0.001$, stress=0.18) (Fig. S5B). The stress levels of the NDMS make the interpretation of the results difficult and show that these values indicate complex relationships between the different communities. The COI primer set, however, indicated strong differences for the community composition ($F=6.47$, $R^2=0.55$, $p<0.001$, stress=0.14) (Fig. 4C) and especially relative read abundance ($F=22.28$, $R^2=0.75$, $p<0.001$, stress=0.12) (Fig. S5C) across the zooplankton samples collected in cold, intermediate and warmer Svalbard marine environments. The variation in the COI zooplankton data are explained by location for 55 and 75%, respectively, an indication that location is the strongest driver for the variation in the dataset.

These results were driven by the presence of highly abundant species, such as *Calanus finmarchicus*, *Oithona similis* and *Parasagitta elegans* on the warmer west side, and *Semibalanus balanoides* and *Catabalema vesicarium* on the cold east side.

The plankton samples that were collected for morphological identification showed similar trends for *Oithona similis* and barnacle larvae (*Cirripedia nauplii*, most likely *S. balanoides*) to the eDNA data (Table S5). For *C. finmarchicus* and *C. glacialis* this could not be assessed as these were not identified to the species level using the applied methodology. The jellyfish, *C. vesicarium*, was not identified in the

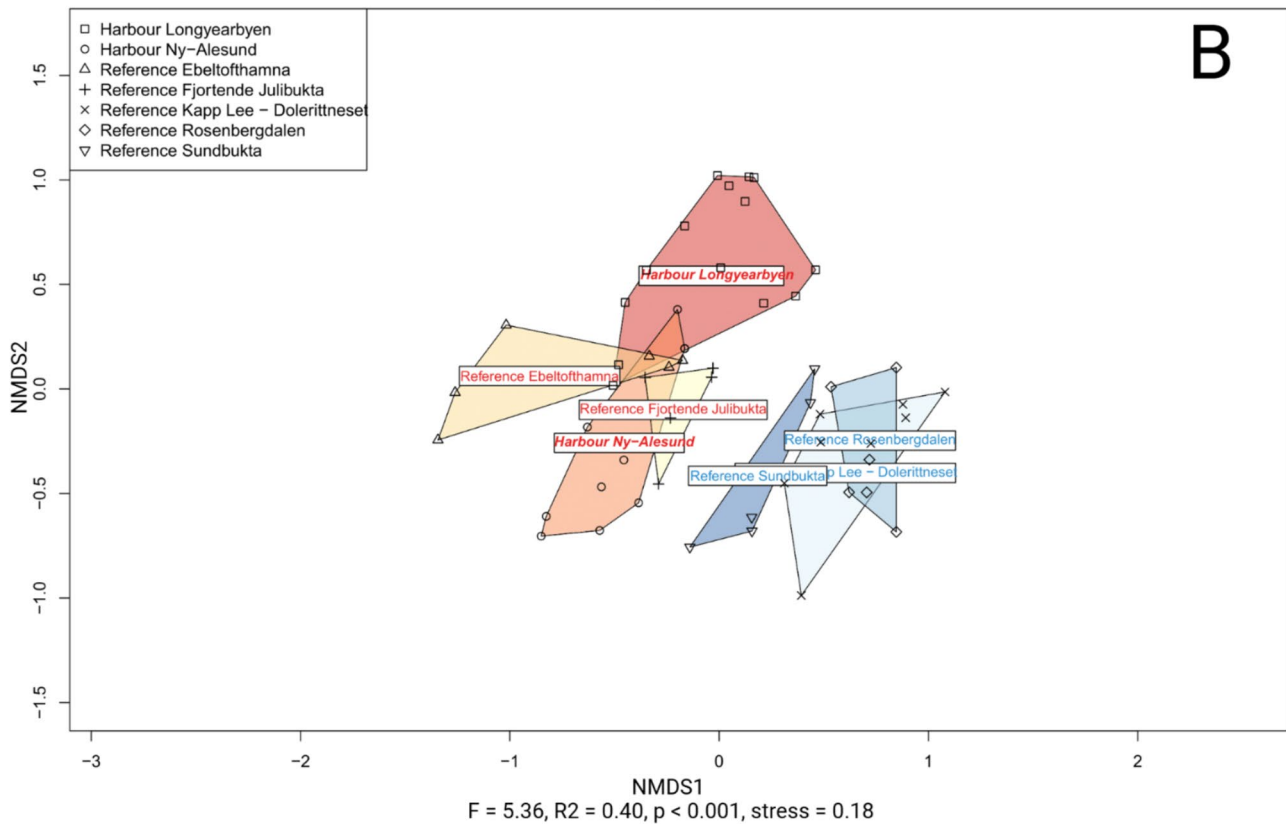
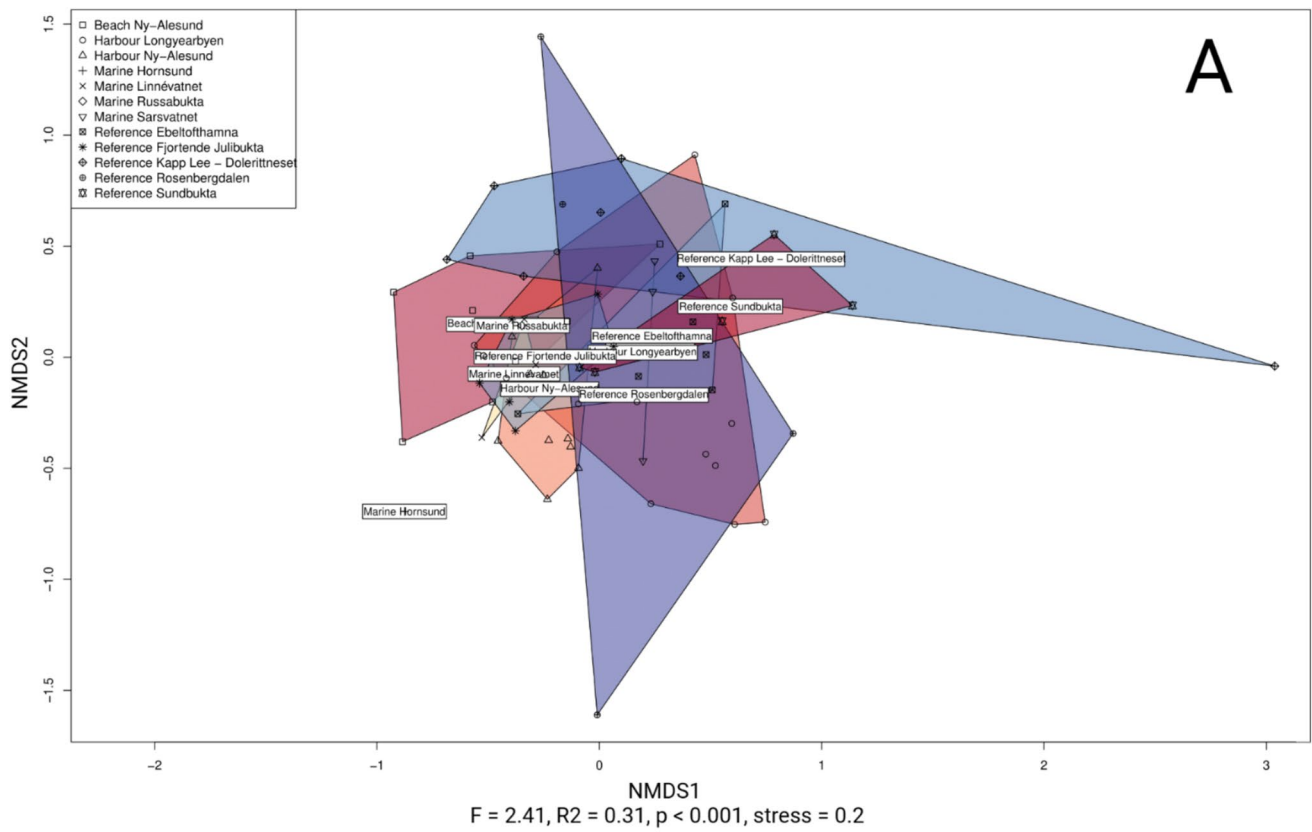


Fig. 2 Nonmetric multidimensional scaling (NMDS) ordination of the community across cold (blue), intermediate (light orange) and warmer (dark orange and red) in eDNA samples collected in surface water in marine coastal areas around Svalbard and analysed using (A) the fish community based on the combined 12S MiFish and 16S Fish primer sets, and (B) the marine community using the COI primer set using presence/absence results

taxonomic samples, probably because the sampling procedure for these samples was not suitable to preserve jellyfish properly (Haddock, 2004). On the other hand, the higher abundance of Cypris (ostracods) in the taxonomic samples (Table S5) was not observed in the eDNA data, which may be a consequence of poor coverage in the DNA data library.

Discussion

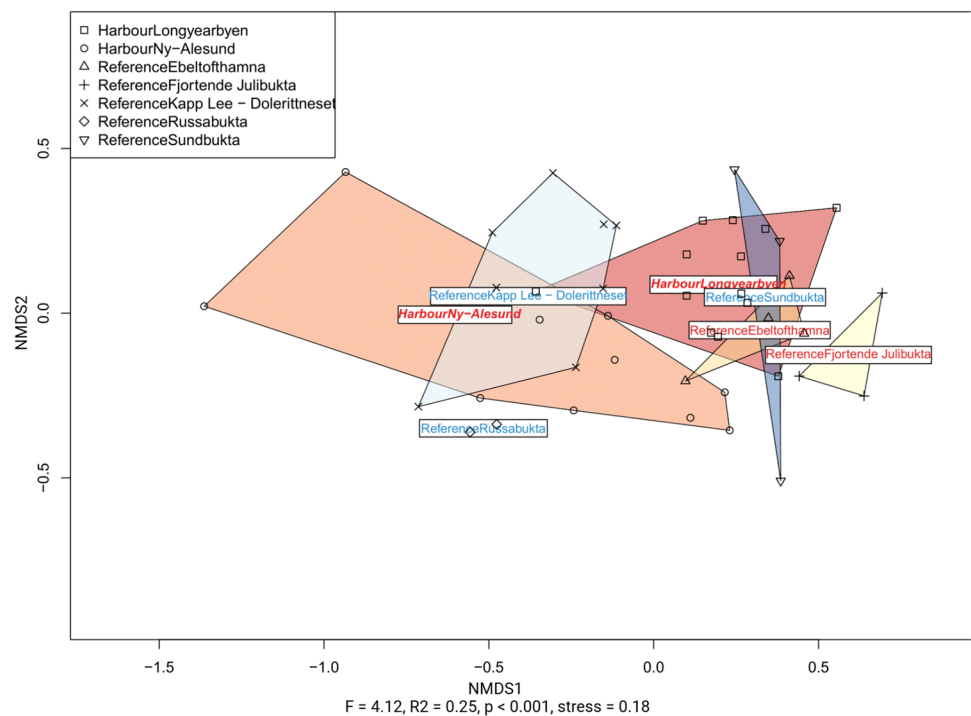
Biomonitoring in the Arctic is challenging, time-consuming, and often seasonally restricted (Beamish et al. 2020; Christensen et al. 2020; Culp et al. 2012; Eriksen et al. 2018; Johnson et al. 2015). Here, we showed that eDNA-based monitoring can be used as a reliable and non-invasive monitoring approach allowing detection of both vertebrate and invertebrate organisms across cold, intermediate and warmer marine habitats in Svalbard's. However, we identified important trade-offs regarding the efficiency of species detection depending on the sampled medium and primer set used. Despite this, when combining optimal sampled media and metabarcoding primers, we highlight that eDNA metabarcoding can be used as a proxy to monitor impacts of marine temperature increases, by uncovering differences in community composition across sites exhibiting different levels of warming, and by identifying potential bioindicator species reflecting environmental changes in Svalbard's marine ecosystems (Tables S1, S2, S3, S4, S5, S6) (Jeunen et al. 2019; Song and Liang 2023; Yang and Zhang 2020).

Using eDNA, we successfully detected taxa belonging to diverse taxonomic groups. We were able to obtain these results through joining a science-tourism expedition, coupled with short-term coastal fieldwork, where we managed to collect 63 marine, 43 sediment and 53 zooplankton samples spanning four areas that included relatively cold, intermediate and warmer marine coastal areas in Svalbard. This led to the detection of the highly diverse marine species community, highlighting the power of eDNA metabarcoding, allowing the generation of large biodiversity datasets through the analysis of environmental samples in a short time frame (Bessey et al. 2020; Euclide et al. 2021; Rupert et al. 2019; Sahu et al. 2025). While we suggest that metabarcoding can serve as a comprehensive tool to monitor Arctic biodiversity, it should be noted that this method relies on the availability of strongly curated and public databases to identify the amplified and sequenced DNA fragments

(Blackman et al. 2022; Claver et al. 2023; Dziedzic et al. 2023; Jeunen et al. 2022; Leray et al. 2022; Marques et al. 2021; Shea et al. 2023; Takahashi et al. 2025). A future reanalysis of the detected OTUs and ASVs sequences using updated databases could therefore result in the detection of potential NIS or species unknown to be present in Svalbard marine environments.

Various studies have highlighted trade-offs between using different metabarcoding primer sets, which often show contrasting performances when amplifying DNA from different taxa, and species discrimination power (Zhang et al. 2020). As the use of a single metabarcoding primer set can introduce biases and potential false-negative results, we used multiple primer sets to optimise biodiversity recovery across taxonomic groups and habitats (Kumar et al. 2022; Macher et al. 2023; Zhu and Iwasaki 2023; Espinosa Prieto et al. 2024). The primers that we used in this study have been designed to amplify either fish (12S MiFish and 16S Fish) (Miya et al. 2015; Nester et al. 2020), metazoan (COI) (Leray et al. 2013), or general eukaryotic organisms (18SV4 and 18SV9) (Amaral-Zettler et al. 2009; Stoeck et al. 2010). This explains the strong variation in species detection within a given sample type depending on the combination of primer sets. Indeed, studies using these different metabarcoding primers often have different aims, and while 18SV4 and 18SV9 primer sets targeting, respectively, the V4 and V9 regions have been successfully used to monitor seasonal changes of plankton community in marine habitats (Almandoz et al. 2024; Lin et al. 2024), the COI primer set has been used to assess general metazoan communities, providing a broad understanding of the marine environments investigated and ecosystem functions (Jeunen et al. 2019; McClenaghan et al. 2020; Holman et al. 2022). However, it should be noted that due to its slow-evolving and conserved regions targeted, the 18S metabarcoding region targeted to identify and detect metazoans can lead to biased results (Tang et al. 2012; Wu et al. 2015; Wangenstein et al. 2018; Questel et al. 2021; Murray et al. 2025). Indeed, in some cases, closely related species show no variation on the amplified metabarcoding fragment, leading to misidentification and potential false-negative or false-positive detection. The 12S and 16S primers targeting fish communities are however more generally used towards biomonitoring in at-risk or protected areas, conservation or fisheries research (Stat et al. 2018; Jerde et al. 2019; Gold et al. 2021; Miya 2022; He et al. 2023). The three fish species that were identified at all locations consisted of two Arctic (*Boreogadus saida*, *Liparis fabricii*) and one predominantly boreal species (*Myoxocephalus scorpius*; according to Karamushko 2008; Table S7). Furthermore, fish species that were found at all locations, except for Hornsund, consisted of predominantly Arctic (*Gymnocanthus tricuspis*) and predominantly boreal species (*Cyclopterus lumpus*, *Lumpenus lampretaeformis*,

Fig. 3 Nonmetric multidimensional scaling (NMDS) ordination of the marine community across cold (blue), intermediate (light orange) and warmer (dark orange and red) marine sediments collected from coastal waters around Svalbard and analysed using the COI primer set using presence/absence results



Clupea harengus, *Gadus morhua*, *Mallotus villosus*, *Pollachius virens*), with the latter four being described as of commercial value in the Barents Sea and increasingly reported on the west coast of Svalbard (Lebel et al. 2025). Other fish of commercial value were found at fewer locations: *Melanogrammus aeglefinus* (Kongsfjorden, Krossfjorden, Isfjorden), *Platichthys flesus* (Isfjorden) and *Salmo salar* (Kongsfjorden, Isfjorden). These observations support the relevance of eDNA techniques for obtaining information on fish distributions around Svalbard.

Despite the use of these combined primer sets, we cannot rule out a potential false-negative detection (Fig. S7). Indeed, potential non-indigenous species from which DNA was detected earlier or that are currently spreading in Svalbard, such as the harpacticoid copepod *Euterpina acutifrons*, the ascidians *Botrylloides violaceus* and *Molgula manhattensis*, and the pink salmon *Oncorhynchus gorbuscha* (van den Heuvel-Greve et al. 2021; Bengtsson et al. 2023; Lennox et al. 2023), were not detected in our study. This could be due to low levels of DNA released by rare targets, slight changes in the sampling or laboratory protocol, insufficient replicate numbers or preservation strategy, inhibition, eDNA decay, low volume of filtered water, stochasticity of the eDNA distribution in the water column or sediment, or gaps in the reference database (Li et al. 2018; Mauvisseau, Burian, et al. 2019; Lance and Guan 2020; Burian et al. 2021; Mauvisseau et al. 2021; Holman et al. 2022; Feng et al. 2023; Anmarkrud et al. 2025). While such factors have previously been shown to lead to false-negative detection, eDNA metabarcoding remains a promising tool

for biodiversity monitoring and early detection of invasive results, especially in the fast-changing Arctic systems (Klymus et al. 2017; W. Feng et al. 2019; Westfall et al. 2020; Wu et al. 2023).

Our eDNA analysis of marine water and sediment samples revealed significant differences in communities between the investigated locations. This agrees with previous eDNA metabarcoding studies conducted in Svalbard (Willassen et al. 2022; Murray et al. 2025) that found different communities across the sampling locations. This was consistent across the primer sets used, suggesting a large variation of the organisms detected across the three different thermal regimes, but could also be due to eDNA transport through different currents (Collins et al. 2018; Andruszkiewicz et al. 2019; Jo et al. 2025). However, the stress levels of the NMDS indicate complex relationships between the different communities, and inhibition coupled with limited sampling could have led to false-negative detection of low-abundance taxa. Mitigating such inhibition with the increase of spatial and temporal sampling resolution, as well as natural and technical replicates could lead to an increased heterogeneity of the fish and invertebrate community across sampling locations and facilitate results interpretation. Analyses of the zooplankton community composition suggest that temperature-associated or current-driven environmental gradients (cold, intermediate, and warmer regions) significantly influence the invertebrate community structure detected (Fig. 4). This was consistent across the 18SV4 and 18SV9 primer sets and especially visible using the COI primer set when using relative read abundance (Fig. S5C).

Particularly, the copepod *C. finmarchicus* was associated with the northwest, which is strongly influenced by the warmer Atlantic current (Fig. S1 and Fig. S2). Our data hereby confirm the validity of the copepod species *C. finmarchicus* as a climate-indicator species for the waters around Svalbard (Choquet et al. 2017; Hop et al. 2019; Søreide et al. 2020), with *C. glacialis* more representative as an Arctic shelf species (Choquet et al. 2017). Furthermore, meroplankton species, such as the barnacle *S. balanoides*, could act as a suitable indicator in water or pelagic zooplankton samples, based on its later reproduction time in colder areas. Such a delay in seasonal development of meroplankton has been described before, e.g., for Rijpsfjorden, northeast Svalbard (Weydmann-Zwolicka et al. 2021). When generating species distribution maps of these potential bio-indicator species using publicly available GBIF records (Fig. S1 and Fig. S2), they showed that these records were limited for the Svalbard area. This is due to restricted data availability for these species in GBIF and could potentially be mitigated using other complementary databases (Choquet et al. 2017). The use of GBIF records led to a relatively poor resolution of these species' presence compared to their expected distribution based on previously known studies (Kwasniewski et al. 2003; Strand et al. 2020).

Here, we collected various types of eDNA samples over a short period of time, leading to a snapshot of biodiversity in the sampled environments. Regular sampling will further assist in the identification of bioindicator species as various studies have highlighted the potential of time series analysis of eDNA samples (Carvalho et al. 2024a, b; Mahlangu et al. 2025). Combined with multi-marker metabarcoding analysis, regular sampling will also further allow diagnosing environmental changes in remote or ice-covered Arctic regions where traditional monitoring is currently restricted (Geraldini et al. 2024; Murray et al. 2025). Additionally, future studies aiming to investigate their presence and abundance along the archipelago should upload these records in GBIF to ensure an increased availability of all published datasets by researchers in a structured way. Additionally, despite the interesting insight provided through the relative read abundance analysis in our study, it remains unknown whether such effects are the results of potential primer biases, leading to an artificial inflation of reads towards specific species, therefore artificially leading to an overrepresentation of taxa. However, the presence/absence patterns reflect known species-specific thermal tolerances despite the poor resolution of these species' distribution maps. In addition to providing early evidence for biogeographical structuring

in Arctic ecosystems, these findings could indicate ongoing ecological changes consistent with Arctic Borealization. Such results therefore allow us to study potential shifts in community structure or zooplankton presence due to temperature changes.

eDNA sampling is a relatively straightforward process that requires minimal equipment and limited specialised taxonomic knowledge (Minamoto et al. 2021; Veilleux et al. 2021). This makes it accessible for citizen science initiatives where non-specialists can easily be engaged with little training, allowing widespread monitoring far beyond what smaller teams of highly trained experts could complete on their own (Larson et al. 2020; Agersnap and Thomsen 2022; Johnston et al. 2023; Knudsen et al. 2023; Leerhøi et al. 2024). eDNA-based metabarcoding therefore offers a strong promise for Arctic biodiversity monitoring but remains prone to trade-offs and limitations, as detection probability varies with organismal abundance, DNA shedding rates, degradation rates, amplification biases as well as reference database coverage (Deiner et al. 2017; Takahashi et al. 2023; Sahu et al. 2025). Best field and laboratory practices allow mitigation of false-positive and false-negative detection to some degree, but researchers and decision makers should remain aware of the risks associated with molecular-based monitoring (Burian et al. 2021), further highlighting the necessity of combining such monitoring tools with traditional surveys. Additionally, we suggest that funding of integrated taxonomy studies in understudied areas such as the Arctic is needed to improve databases, and thus the accuracy of molecular monitoring studies. Despite this, such surveys can greatly increase our understanding of Arctic ecosystems, allowing better monitoring of the fast changes currently ongoing, and recent advancement toward the inclusion of natural samples such as marine sponges, including the ones stored in museum collections, or eRNA monitoring potential could allow better characterisation of both spatial and temporal diversity (Pochon et al. 2017; Giroux et al. 2022; Harper et al. 2023; Cai et al. 2024; Corral-Lou et al. 2025; Jeunen et al. 2026).

Here, we found out that eDNA analysis identified temperature or location-associated biodiversity, and potential bioindicator species in plankton samples. We therefore recommend that future studies aiming to investigate environmental gradients in Arctic marine systems focus on eDNA analysis of plankton samples, in addition to other sample types such as water and sediment that are applied more often. Our results further highlighted the added value of multi-marker analysis, improving biodiversity recovery and mitigating potential false-negative detection.

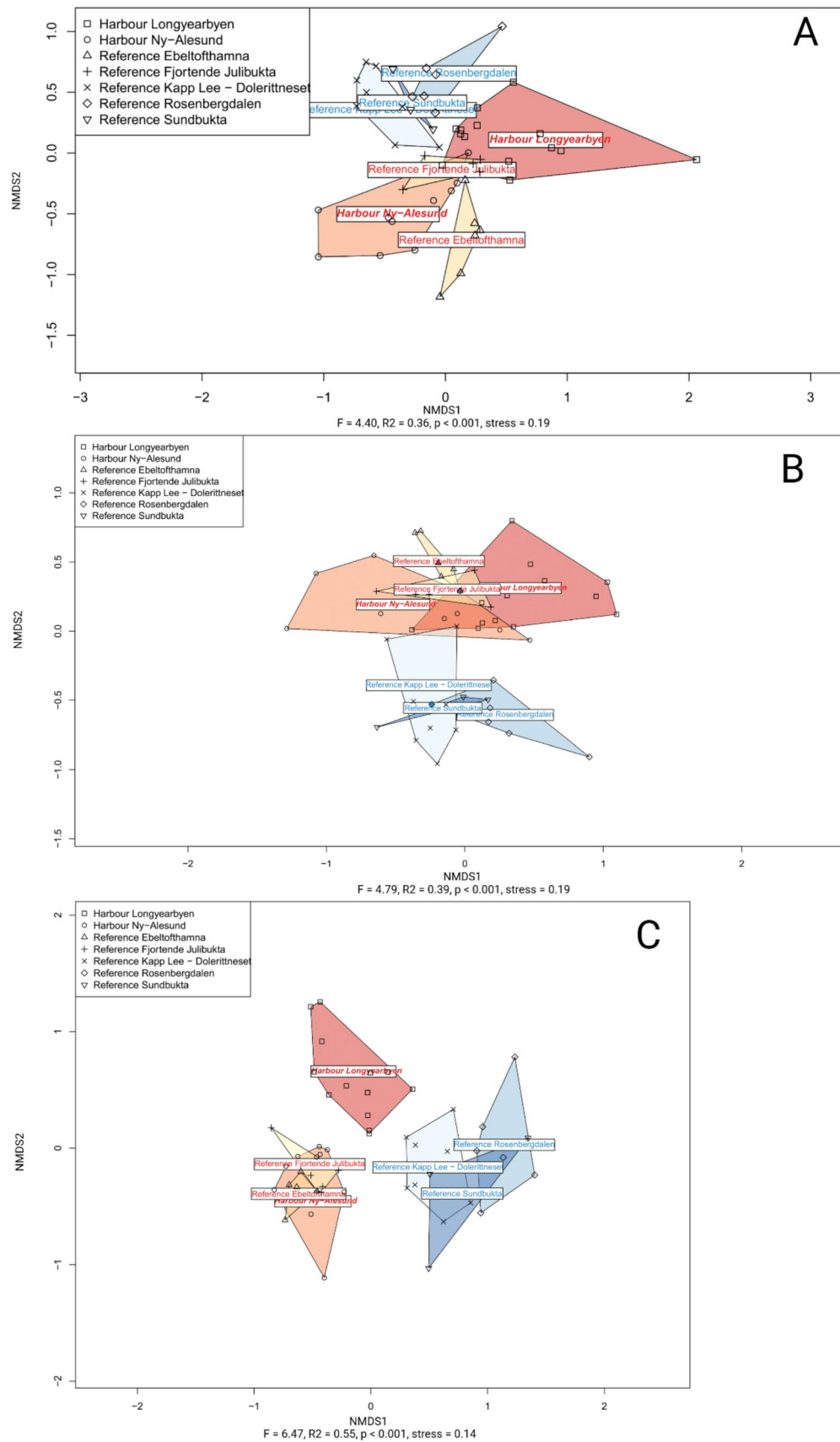


Fig. 4 Nonmetric multidimensional scaling (NMDS) ordination of the marine community across zooplankton samples collected in the Arctic (blue), the intermediate (light orange) and the Atlantic (dark orange and red) marine environments in Svalbard using presence/absence results with the (A) 18SV4 primer set, (B) 18SV9 primer set and (C) COI primer set

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00300-026-03488-9>.

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Author Contributions Conceptualization: MvdHG, IMM, PER, HdB and QM; Sampling: MvdHG, IMM, HV and QM; Laboratory analysis: MP, AGdG, LK and ASN; Bioinformatics: MP; Data curation: MP and QM; Statistical analysis: MP; Original draft: MvdHG, MP and QM; Review and editing: all authors; Funding acquisition: MvdHG, IMM, PER, HdB and QM.

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Data availability Raw sequencing data and metadata can be found here: <https://zenodo.org/records/16636529> and <https://zenodo.org/records/16639855>, all additional information can be found in the supplementary information.

Declarations

Conflict of interest The authors declare no competing interests.

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