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ORIGINAL ARTICLE

Investigating pelagic biodiversity and gelatinous zooplankton communities in the rapidly changing European Arctic: An eDNA metabarcoding survey

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Abstract

Fram Strait, the gateway between the Arctic and Atlantic Oceans, is undergoing major climate change-induced physical and biological transformations. In particular, rapid warming and ongoing "Atlantification" are driving species range shifts and altering food web structures in the Arctic. Understanding and predicting the consequences of these processes on future ecosystems requires detailed assessments of local and pelagic biodiversity. Gelatinous zooplankton (GZP) is an important component of pelagic communities, and recent evidence indicates that such communities are undergoing major changes in the Fram Strait. However, as sampling GZP is challenging, they are regularly underestimated in biodiversity, distribution, and abundance. To overcome this and address existing ecological knowledge gaps, we investigated patterns of pelagic metazoan diversity in Fram Strait using environmental DNA (eDNA) metabarcoding of the cytochrome *c* oxidase I (COI) gene. We successfully detected a broad range of taxa from the marine metazoan and GZP communities across sampling locations and ocean depth zones. We demonstrate the vertical structuring of diversity and elucidate relationships between taxa and water mass indicators, such as salinity and temperature. Furthermore, when comparing eDNA data with net and video transect data for GZP at the same period and location, we found that eDNA uncovered a higher number of taxa, including several that were not detected by the other methods. This study is a contribution to the formation of baseline Arctic GZP biodiversity datasets, as well as future research on changing marine metazoan biodiversity and community composition.

KEYWORDS
Arctic Ocean, deep sea, environmental DNA, Fram Strait, jellyfish, open ocean

1 | INTRODUCTION

The Arctic is undergoing rapid and unprecedented transformations because of anthropogenic climate change. It is warming four times faster than the global mean (Rantanen et al., 2022), which is evidenced by the rising sea surface temperatures and declining perennial sea-ice cover observed in recent decades (Huang et al., 2017; Rantanen et al., 2022). The largest source of oceanic heat into the central Arctic is the Fram Strait (Beszczynska-Moeller et al., 2011), which is known as the Atlantic gateway to the Arctic. This hydrographically dynamic strait is the only deepwater inflow into the Arctic Basin, acting as the transition between Atlantic-boreal and high-Arctic biogeographic zones (Hop et al., 2019). The "Atlantification" of the Arctic, underpinned by increasing volumes and temperature of northward flowing Atlantic water, is having growing influences on both physical and biological processes in the region, and its impacts are predicted to increase drastically in the coming years (Ingvaldsen et al., 2021; Polyakov et al., 2017, 2020). Biodiversity-linked consequences of this Atlantification, such as shrinking habitat ranges of Arctic- and northward encroachment of Atlantic species have been observed in phytoplankton (Neukermans et al., 2018; Oziel et al., 2020), zooplankton (Csapó et al., 2021; Ingvaldsen et al., 2021) and fish (Polyakov et al., 2017). Changes in species' distribution ranges and the subsequent increases in the number of boreal-Atlantic species and biomass are leading to the restructuring of Arctic ecosystems (Basedow et al., 2018; Csapó et al., 2021). The collection of baseline datasets with biodiversity surveys is crucial in the establishment of long-term monitoring for understanding climate-change impacts on marine ecosystems. These will allow us to document and track species distribution shifts in the Arctic Ocean, particularly in the major gateways connecting it with temperate regions.

Zooplankton are a crucial link between primary producers and higher trophic levels, and they play a pivotal role in the biological carbon pump. The zooplankton community in Fram Strait typically consists of a mix of "true" Arctic, Arctic-boreal, and boreal-Atlantic expatriates (Weydmann et al., 2014). The distribution, composition, and food-web structure of these communities is heavily influenced by environmental factors such as sea-ice cover, temperature, salinity, and nutrient supply (Gluchowska, Dalpadado et al., 2017; Wassmann et al., 2015). For instance, the abundant Arctic copepod *Calanus glacialis* is typically associated with colder temperatures and higher sea-ice coverage, whereas its boreal congener *C. finnmarchicus* is an indicator of warmer temperatures and Atlantic water masses (Hatlebakk et al., 2022). An important component of the pelagic community is the gelatinous zooplankton (GZP), or jellyfish, a polyphyletic and highly diverse group including cnidarian medusae, ctenophores, and pelagic tunicates. They serve major ecosystem roles as predators and are important in pelagic-benthic coupling and vertical carbon export (Jaspers et al., 2023; Lebrato et al., 2012, 2013), particularly when occurring in high numbers (aggregations or blooms). Recent studies have shown poleward expansions of the distribution ranges of boreal species, e.g., for the large scyphozoan *Periphylla periphylla* around Svalbard and in the Nansen Basin (Geoffroy et al., 2018; Ingvaldsen et al., 2023). Additionally, increased abundances of the arcto-boreal hydrozoan *Aglantha digitale* have been found in warmer water masses in the North Atlantic (Haberlin et al., 2019) and in Atlantic water masses in Fram Strait (Mańko et al., 2020), where it is predicted to become a dominant species as the Arctic warms (Mańko et al., 2020; Pantiukhin et al., 2023a). In contrast, "true" Arctic species are predicted to experience significant decreases in abundance in coming decades, as shown for the midwater hydrozoan *Sminthea arctica* (Pantiukhin et al., 2023a). Overall, an increase in GZP abundances but a decrease in GZP richness has been projected under future climate-change scenarios (Pantiukhin et al., 2023a), which makes this group an important candidate for zooplankton monitoring efforts.

Despite an increase in studies with a focus on GZP diversity and distribution in the Arctic, sampling limitations to typical survey methods remain. Successful detection of different taxa varies among the type of trawl or net used (Hosia et al., 2017; Nogueira Júnior et al., 2015), as they can destroy more delicate specimens or capture only a limited size range. While optical methods can detect individuals without damaging them and hence provide more reliable abundance estimates for some taxa (Pantiukhin et al., 2023a), they also have known biases (Hosia et al., 2017; Raskoff et al., 2010) and can be resource-intensive and deployed only in limited spatial areas. To fill in the knowledge gaps on GZP diversity in the Arctic and improve monitoring efforts to document ongoing species shifts, there is an urgent need for time- and cost-effective methods that can yield a high taxonomic resolution and be implemented at various spatial and temporal scales.

Metabarcoding of environmental DNA (eDNA) has become an efficient and non-invasive approach increasingly used in impact assessments, biodiversity and community structure surveys, species-specific detection, and biosecurity applications in the last decade (Bunholi et al., 2023). It is highly sensitive, allows for non-invasive detection, and can provide high resolution of taxonomic identification without the necessity of expert taxonomic knowledge. The efficacy of eDNA metabarcoding as a tool to monitor metazoan biodiversity has been validated against traditional methods in various marine habitats (Djurhuus et al., 2018; Feng et al., 2022; Govindarajan et al., 2021; Lacoursière-Roussel et al., 2018; Suter et al., 2021). While there has been an increasing number of studies using eDNA to detect GZP in recent years, they have largely been focused on single-species detection rather than metabarcoding (Bolte et al., 2021; Minamoto et al., 2017; Morrissey et al., 2022; Ogata et al., 2021; Takasu et al., 2019) and GZP community studies with eDNA are so far missing. Furthermore, the application of eDNA metabarcoding to specifically assess GZP biodiversity in polar regions is yet to be implemented.

In this study, we provide the first assessment of the pelagic marine metazoan community in the rapidly changing Fram Strait using metabarcoding of the mitochondrial COI fragment. The aim of this research was to (i) survey marine metazoan biodiversity across the Fram Strait, (ii) investigate GZP alpha and beta diversity and the environmental drivers of community composition across polar- and

temperate-derived water masses, and finally (iii) compare the efficacy of eDNA metabarcoding as a survey method for GZP to other sampling and observational approaches, including net caught specimens and in situ camera transects.

2 | MATERIALS AND METHODS

2.1 | Study area and sample collection

Samples were collected in May and June of 2021 during the oceanographic cruise PS126 (Soltwedel, 2021) of the R/V Polarstern (Knust, 2017). Seven locations were sampled in the HAUSGARTEN observatory, with two in the East Greenland Current (EG1 and EG4), three in central Fram Strait (HG4, N4, and S3), and two on the West Spitsbergen Shelf (SV2 and SV4) (Figure 1a). At each location, seawater samples for metabarcoding were collected at specific depths throughout the water column (all stations: 0, 20, 50, 100 m; deep stations additionally: 200, 400, 500, 750, 1000, 1300, 1600, 2000, 2250, and 2500 m), using 12 L Niskin bottles mounted on a conductivity-temperature-depth (CTD) Rosette. Sterilized canisters were filled with 6 L of water from a single Niskin per depth, from which triplicate 2 L samples were taken, resulting in a total of 194 samples (Table S1). The 2 L samples were filtered through 0.22 µm Sterivex-GP filters (Merck Millipore) using a Masterflex peristaltic pump. Field blanks were taken by filtering MilliQ water across one filter per CTD cast. New tubing was used for each depth when collecting water from the Niskin bottles and during filtering. All work benches and other necessary lab equipment were sterilized with a 10% bleach solution, followed by MilliQ water in between stations and the plastic canisters between samples. Filters were stored at −80°C until laboratory processing.

Hydrographic data was obtained simultaneously with water collection at each station using an SBE911+ CTD sensor mounted on the rosette water sampler. Water masses were determined based on temperature and salinity measurements modified from Rudels et al. (2013) (Table S2). Depth zones were classified as upper-epipelagic (0–99 m), lower-epipelagic (100–200 m), mesopelagic (201–1000 m), and bathypelagic (>1001 m).

Samples for morphological identification were collected using a Maxi-Multinet (Hydrobios) and Bongo plankton nets (Hydrobios). Depth-stratified Multinet hauls, with 330 µm mesh size, were carried out vertically between 2500 m and the surface at a wire speed of 0.5 m/s. At most stations, we carried out oblique Bongo net tows, with mesh sizes of 335 and 500 µm, equipped with a large non-filtering cod-end and a V-Fin depressor, deployed between 100 and 740 m depths, at a speed of 2 knots. At station N4, vertical Bongo net hauls were carried out due to heavy ice cover. Specimens were identified to the lowest possible taxonomic level on board using taxonomy keys (Bouillon et al., 2006; Licandro et al., 2017; Licandro & Lindsay, 2017). Damaged or ambiguous specimens were only identified at higher taxonomic levels to avoid misidentification (e.g., order Trachymedusae).

Video data were obtained by deploying the Pelagic In Situ Observation System (PELAGIOS) (Hoving et al., 2019), during horizontal transects at three of the stations. All data for video observations were taken from the publicly available dataset on PANGAEA (Pantiukhin et al., 2023b). We used GZP presence data from all

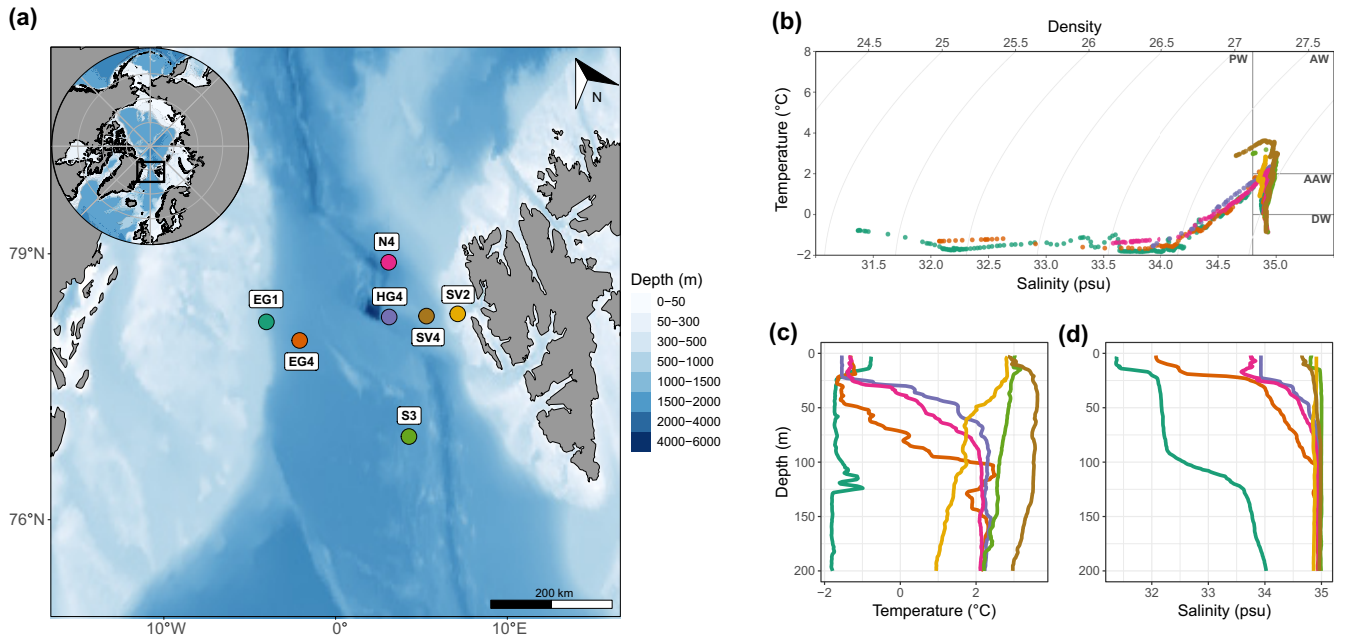

FIGURE 1 Study sites and oceanographic profiles. (a) Map of the seven sampling locations in Fram Strait. (b) Temperature-Salinity plot of the entire water column at each station, with indicated water masses defined as Polar Water (PW), Atlantic Water (AW), Arctic Atlantic Water (AAW), and Deep Water (DW). (c) Temperature (°C) and (d) salinity (psu) of upper 200 m of all stations. Colors of profiles and points correspond to station colors on the map.

depths combined at each station for comparison with the eDNA data from the present study and the available net data (Havermans et al., 2021).

2.2 | eDNA extraction, library preparation, and sequencing

Environmental DNA was extracted using the DNeasy Blood and Tissue kit (QIAGEN) according to the manufacturer's protocol, with small modifications as described in Visser et al. (2021). DNA was diluted in 2 × 50 μL AE Buffer, and extraction blanks were taken during every extraction. All equipment and benches were cleaned in between extractions using a 1:10 Bleach and MilliQ solution, followed by a MilliQ rinse, 70% ethanol, and finally treated with UV light for a minimum of 1 h. Immediately before and during the extractions, DNA/RNA-ExitusPlus (AppliChem) was used for sterilizing equipment. The DNA extracts were stored at −20°C for further processing.

The DNA metabarcoding library preparation and sequencing were carried out by AllGenetics & Biology SL, Spain (www.allgenetics.eu). In order to amplify DNA of as many marine metazoans as possible, we used the common universal metazoan 313 bp mitochondrial cytochrome oxidase *c* subunit 1 (COI) barcode, known as the "Leray" fragment. This barcode has been successfully implemented to detect a broad array of marine taxa, including GZP (Antich et al., 2022; Dischereit et al., 2022; Urban et al., 2022). The forward primer is mlCOIintF-XT: (5′GGWACWRGWTGRACWITITAYCCYCC3′) (Wangensteen et al., 2018) and the reverse primer jgHCO2198: (5′TAIACYTCIGGRTGICCRAARAAYCA3′) (Leray et al., 2013). The PCR master mix for the first PCR step consisted of 2.5 μL of template DNA, 0.5 μM of the primers, 6.25 μL of Supreme NZYTaq 2x Green Master Mix (NZYTech), and ultrapure water with a final volume of 12.5 μL. The PCR cycle included an initial denaturation step at 95°C for 5 min, followed by 35 cycles of 95°C for 30 s, 54.7°C for 45 s, 72°C for 45 s, and a final extension step at 72°C for 7 mins. In the second PCR step, oligonucleotide indices were attached with the same conditions as the first but with five cycles and an annealing temperature of 60°C. PCR controls were included in each PCR to check for contamination during library preparation. Library size was verified on 2% agarose gels stained with GreenSafe (NZYTech)and purified using ag-Bind RXNPurePlus magnetic beads (Omega Biotek), according to the manufacturer's protocol. The concentration of the final libraries was checked on a Qubit dsDNA with the HS Assay (Thermo Fisher Scientific) before pooling at equimolar amounts. The final pool was sequenced on a PE250 flow cell (Illumina) on a NovaSeq platform (Illumina), aiming for a total output of 27 gigabases and a high target sequencing depth per sample (500,000 bp). In order to increase the chances of detecting rare taxa, we chose to use the NovaSeq platform for greater sequencing depth and improved performance of the flow cell compared to the MiSeq platform (Singer et al., 2019).

2.3 | Bioinformatics

We applied a metabarcoding pipeline based on OBITOOLS version 1.01.22 (Boyer et al., 2016), following Antich et al. (2021) to process the raw sequences. Pair-end reads were assembled using *illuminapairedend*, and those with median phred quality scores <40 were discarded. Demultiplexing and primer removal were done using *ngsfilter*. Length filtering (299–320 bp) and the removal of sequences containing erroneous bases were done with *obigrep*, and sequence dereplication with *obiuniq*. We used the *Uchime-denovo* algorithm in VSEARCH (Rognes et al., 2016) to remove chimeric sequences. SWARM 3.0 (Mahé et al., 2015) was used to cluster the remaining sequences into molecular operational taxonomic units (MOTUs) with a *d* value of 13. Taxonomic assignment was done with the *ecotag*, using a local reference database consisting of 174,544 COI sequences from Genbank, BOLD, and in-house sequences (available at: https://github.com/uit-metabarcoding/DUFA/). We used the LULU algorithm (Frøslev et al., 2017) as a post-clustering filter to remove any remaining erroneous MOTUs. Blank correction followed with the removal of MOTUs that were present in blank or control samples at more than 10% of their total read abundance (Table S3). To reduce the impact of tag-jumping but still allow the possibility to detect rare MOTUs, we applied a minimum threshold abundance of 0.0005% to each sample before removing any remaining MOTUs with less than 5 reads. One sample failed in sequencing and was removed from the dataset. The assignments of the remaining sequence annotations were further improved where possible by using BOLDigger (Buchner & Leese, 2020) and the BOLD database (http://www.barcodinglife.com) (Ratnasingham & Hebert, 2007). For this, we modified the sequence similarity thresholds and adjusted the taxonomic assignment accordingly. The thresholds used were species (97%), genus (95%), family (90%), order (85%), class (80%), and phylum (<80%). Finally, MOTUs assigned as prokaryotes, terrestrial taxa (e.g., insects), fungi, and phytoplankton were removed, so only marine metazoans with a taxonomic assignment threshold higher than 80% remained.

2.4 | Data analysis

All statistical analyses and data visualizations were conducted in R 4.1.0 (R Core Team, 2021). We pooled triplicates from the same station and depth by summing read counts. Read counts were then normalized to the lowest number observed in the dataset using the scaling with ranked subsampling (SRS) method (Beule & Karlovsky, 2020), with the *srs*() function in the SRS package in R (Heidrich et al., 2021). In order to avoid the impact of sampling biases between stations with different sampling intensities (shallow stations: surface—max. 100 m; deep stations: surface—max. 2500 m), we split the metazoan MOTU dataset for alpha diversity analyses into (1) the upper 100 m of all seven stations, and (2) all ocean zones at deep stations only (EG4, HG4, N4, and S3). The alpha diversity analyses for the GZP dataset were only calculated on the four deep stations due to low or no GZP detections at

the other stations. To analyze differences in diversity across the sampling locations and depth zones, we calculated the Shannon-Wiener index and species richness based on normalized MOTU data using the *vegan* package v.2.5-6 (Oksanen et al., 2019). We compared alpha diversity between depth zones and locations using ANOVA, followed by pairwise comparisons with Tukey's HSD. We calculated species richness on non-rarefied data for the GZP dataset only, for which assumptions of parametric data were not met. In this case, we used Welch's one-way tests and Game-Howell pairwise comparisons.

To investigate differences in community composition across locations and depth zones, beta-diversity analyses were performed for both the metazoan and GZP datasets. We calculated Jaccard distances based on presence-absence data and visualized them with non-metric multidimensional scaling ordination (nMDS) using the *metaMDS*() function in *vegan*. Permutational multivariate analysis of variance (perMANOVA) tests with 999 permutations was conducted to check for significant differences between locations and ocean zones, using the *adonis2*() function. Subsequent pairwise comparisons with Bonferroni adjusted *p*-values were done using *pairwise.adonis*() from the pairwiseAdonis package (Martinez Arbizu, 2020) in R. Data dispersion was performed to check for multivariate homogeneity using the *betadisper*() function.

Correlations between the relative abundances of individual MOTUs and environmental parameters, including water mass indicators, were identified using sparse partial least squares (sPLS) regression analysis. The sPLS was conducted using raw MOTU count data. We removed MOTUs with near zero variance using the *nearZeroVar*() function in the mixOmics package (Rohart et al., 2017) and replaced zeros with pseudo counts of 1. Environmental variables were standardized using the *decostand*() function with the method *standardize* in *vegan*. The sPLS was done using the *spls*() function from mixOmics, with canonical mode and a centered-log ratio transformation. We used the output from the sPLS model to compute pairwise similarity matrices, and the significant correlations were visualized in a heatmap using the *cim*() function.

We compared the efficacy of eDNA with net and optical sampling methods based on taxon richness. To account for divergences in sampling procedures, only presence data recorded from nets and video tows was used rather than abundance data. To investigate the efficiency of eDNA and nets to detect GZP diversity, we compared the taxon richness at each taxonomic level for all stations combined. Furthermore, we compared all three methods (eDNA analysis, net catches, and camera tows) at three stations (EG4, HG4, and S3), where all methods were deployed. To investigate how the detection efficiency of each of the three methods compares at a finer taxonomic level, we used only the MOTUs identified to genus and/or species level for cnidaria but to class level for cydippid ctenophores. This was done to account for known taxonomic uncertainties related to morphological identifications, which was the case for the scyphozoan genus *Atolla* (Matsumoto et al., 2022), the hydrozoan *Botrynema* genus (Montenegro et al., 2023) and the ctenophores belonging to the *Beroe* genus (Shiganova & Abyzova, 2022) and the class Cyddipidia (Majaneva & Majaneva, 2013). The validity of these taxa was further checked against the World Register of Marine Species (WoRMS) available from (https://www.marinespecies.org).

3 | RESULTS

3.1 | Oceanographic properties

The oceanographic properties varied across sampling stations (Figure 1b–d), reflecting the different water masses of the Fram Strait. Temperature values ranged from the highest at 3.6°C at SV4 to the lowest at −1.7°C at EG1 (Figure 1c and Table S1). Salinity values ranged from 31.2 psu at EG1 to 34.9 psu at S3 (Figure 1d and Table S1). Details of all water parameters measured are available in Table S1. In addition to longitudinal shifts in conditions, depth-stratified water bodies were observed (Figure 1b). At stations SV4 and S3, a small layer of Polar Water (PW) occurred in the upper tens of meters, with Atlantic Water (AW), Arctic Atlantic Water (AAW), and Deep Water (DW) below. The deepwater stations HG4 and N4 both had PW close to the freezing point in the top 25 m, as well as AW, AAW, and DW in the lower water column. The top 100 m of EG4 consisted of PW with very low salinities, an AW layer, and AAW and DW formed at depth. EG1 was largely dominated by low salinity PW and some AAW and DW at lower depths.

3.2 | Pelagic metazoan alpha diversity

Sequencing of the COI fragment resulted in a total of 105.5 million sequence reads. After quality control and refinement, 700,000 reads assigned to marine metazoans were kept, representing 239 MOTUs. Rarefaction curves showed that most samples reached a plateau with the obtained sequencing depth (Figure S1). A large diversity of marine metazoans was captured, with the majority of the metazoan sequences assigned to ten phyla (Figure 2a). Arthropoda was the most dominant phyla, making up 84.6% of the metazoan reads in the dataset, followed by Cnidaria (7.56%) and Porifera (1.9%). The remaining phyla consisted of less than 1%, along with unassigned metazoans. We successfully detected most of the marine metazoan groups known to exist in high abundance in the Arctic Ocean, including Annelida (Polychaeta, Sipuncula), Arthropoda (Copepoda, Malacostraca, Ostrocoda), Chordata (Actinopterygii, Ascidiacea, Mammalia), Cnidaria (Anthozoa, Hydrozoa, Scyphozoa), Ctenophora (Nuda, Tentaculata), Echinodermata (Crinoidea, Echinoidea, Holothuroidea), Mollusca (Bivalvia, Cephalopoda, Gastropoda, Scapopoda), and Porifera (Demospongiae, Hexactinellida). The groups with the highest number of reads detected were copepods and cnidarians (Table 1). The highest number of MOTUs were detected in Cnidaria (58), followed by Arthropoda (49), Porifera (35), Annelida (27), and the remaining phyla.

The analysis of alpha diversity indices showed that location did not have a significant effect on the Shannon index [*anova*,

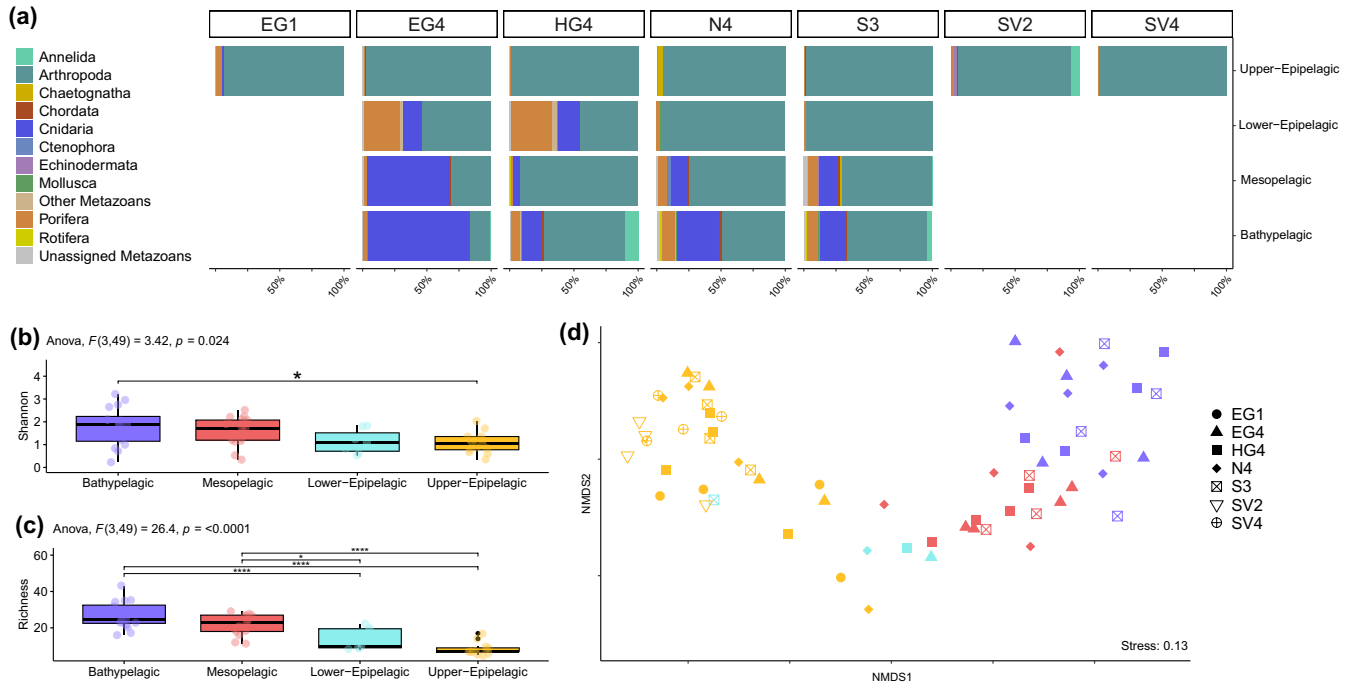

FIGURE 2 Pelagic metazoan alpha and beta-diversity patterns. (a) Relative read abundances of marine metazoan MOTUs phyla at each depth zone and sampling location. (b) Shannon diversity index (*H'*) and (c) species richness of SRS normalized metazoan MOTU data at each depth zone for all four deep stations combined. Tukey's HSD pairwise comparison with Tukey adjusted *p*-values was used. * indicates a significant difference of <0.05 and **** indicates a significant difference of <0.001. (d) Nonlinear multidimensional scaling for community structuring of MOTUs ($K=2$) based on Jaccard distance. Colors indicate ocean zones, and point shape indicates station, stress value displayed on plot. Depth zones are defined as upper-epipelagic (0–99 m), lower-epipelagic (100–200 m), mesopelagic (201–1000 m), and bathypelagic (>1000 m).

DF = (6, 49), $F=2.536$, $p=0.053$], nor on MOTU richness in the upper 100 m of the seven stations analyzed [*anova*, DF = (6,49), $F=2.005$, $p=0.11$]. When comparing the four deep stations, location also did not have a significant effect on Shannon index [*anova*, DF = (3,49), $F=1.273$, $p=0.294$], nor MOTU richness [*anova*, DF = (3, 49), $F=0.083$, $p=0.969$]. However, the depth zone was found to be significantly different on both the Shannon index [*anova*, DF = (3,49), $F=3.417$, $p=0.024$] and MOTU richness [*anova*, DF = (3,49), $F=26.402$, $p \leq 0.01$]. Subsequent pairwise comparisons showed that the bathypelagic zone had a significantly higher Shannon index than the upper-epipelagic zone (Figure 2b). The bathypelagic and mesopelagic zones were found to be significantly higher in MOTU richness than each of the epipelagic layers (Figure 2c).

3.3 | GZP alpha diversity

A total of 53 GZP MOTUs were recovered with more than 80% similarity, of which 51 were cnidarians and two ctenophores. In total, 12 GZP MOTUs were assigned to species level, 14 to genus, 16 to family, 18 to order, and all to class level. Both Ctenophora classes, Nuda and Tentaculata, were detected, five hydrozoan orders (Anthoathecata, Leptothecata, Narcomedusae, Siphonophorae, and Trachymedusae), and three scyphozoan orders (Coronatae, Rhizostomeae, and Semaeostomeae) (Table S4). The most abundant GZP MOTU by read abundance was the mid-water hydrozoan *Botrynema brucei* (39.0% of GZP reads), followed by the siphonophore *Marrus orthocanna* (31.1%), the 33 unassigned hydrozoans (19.5% combined), the deepwater scyphozoan *Atolla tenella* (2.68%) and unassigned Anthoathecata (2.39%). The remaining GZP taxa each made up less than 2% of the detected reads.

When analyzing alpha diversity indices based on rarefied data at the four deep stations, we found no significant effect of location on GZP Shannon index [*anova*, DF = (3, 33), $F=1.745$, $p=0.137$] nor MOTU richness [*anova*, DF = (3, 33), $F=1.904$, $p=0.148$]. Likewise, no significant effect of depth zone on GZP Shannon index [*anova*, DF = (3, 33), $F=1.62$, $p=0.213$] nor MOTU richness [*anova*, DF = (3, 33), $F=2.277$, $p=0.118$] was found. However, given the focus on the smaller GZP component of the dataset (7.56% of total MOTUs), we also analyzed MOTU richness based on non-rarefied data with the goal of retaining rarer taxa. Here, we found that depth zone had a significant effect on GZP MOTU richness (Figure 3b). The subsequent pairwise comparison found that the bathypelagic and the mesopelagic layers had significantly higher richness than the lower- and upper-epipelagic layers, respectively (Figure 3b). Nevertheless, non-rarefied data must be treated with caution as differences in sequencing depth cannot be ruled out as a significant driver behind significant differences.

TABLE 1 Molecular operational taxonomic units (MOTUs) detected in the eDNA dataset had the highest number of reads per phylum.

Phylum (total no. MOTUs)	Family	MOTU name	Depth zone	Location	Biogeographical distribution
Annelida (28)	Pholoidae	*Pholoe assimilis*	U-E	SV2	Arctic-boreal (Degen & Faulwetter, 2019)
	Spionidae	*Laonice* sp.	B	EG4, S3, N4, HG4	
	Trichobranchidae	*Terebellides* sp.	B	HG4	
		Polychaeta_2	B	HG4, S3	
	Golfingiidae	*Nephasoma* spp.	B	HG4	
Arthropoda (49)	Calanidae	*Calanus hyperboreus*	U-E, M, B	EG1, HG4, N4, S3, SV2, SV4	Arctic (Ingvaldsen et al., 2023a)
	Oithonidae	*Oithona similis_2*	All	All	Ubiquitous (Weydmann et al., 2014)
	Calanidae	*Calanus finmarchicus*	All	All	Boreal (Weydmann et al., 2014)
	Clausocalanidae	*Pseudocalanus minutus*	U-E	SV2, SV4	Arctic-boreal (Weydmann et al., 2014)
	Metridinidae	*Metridia longa*	All	EG1, EG4, HG4, N4, S3, SV2	Arctic-boreal (Weydmann et al., 2014)
	Clausocalanidae	*Microcalanus pusillus*	U-E, L-E, M	All	Arctic-boreal (Weydmann et al., 2014)
		Copepoda_5	M, B	EG4, HG4, N4, S3	
	Oithonidae	*Oithona similis_1*	U-E, L-E	All	Ubiquitous (Weydmann et al., 2014)
	Clausocalanidae	*Microcalanus pygmaeus_2*	M, B	EG4, HG4, N4, S3	Arctic-boreal (Weydmann et al., 2014)
	Euchaetidae	*Paraeuchaeta glacialis*	U-E, B	EG1, EG4, HG4	Arctic-boreal (Kosobokova et al., 2011)
	Oncaeidae	*Triconia borealis*	All	All	Arctic-boreal (Weydmann et al., 2014)
	Oithonidae	*Oithona atlantica*	U-E, L-E	EG4, HG4, N4, S3, SV2	Boreal (Wassmann et al., 2015)
		Cyclopoida_2	B	EG4, HG4, N4, S3	
	Calanidae	*Calanus glacialis*	U-E, M, B	All	Arctic (Weydmann et al., 2014)
		Arthropoda_4	All	EG1, EG4, N4, S3, SV4	
Chaetognatha (3)	Eukrohniidae	*Eukrohnia bathyantarctica*	U-E, M, B	EG4, HG4, N4, S3	Ubiquitous (Miyamoto et al., 2012)
	Sagittidae	*Sagitta* sp.	U-E, L-E	EG1, EG4	
	Sagittidae	*Pseudosagitta maxima*	M	EG4	Ubiquitous (Kulagin & Neretina, 2017)
Chordata (12)	Zoarcidae	*Lycodes esmarkii*	B	HG4, S3	
	Clupeidae	*Sardinella maderensis*	M	S3	
	Gadidae	*Boreogadus saida*	U-E, M, B	EG1, HG4, S3	Arctic (Ingvaldsen et al., 2023a)
	Balaenidae	*Balaena mysticetus*	M, B	EG4, N4	
	Gadidae	*Micromesistius poutassou*	B	S3	
Cnidaria (58)	Halicreatidae	*Botrynema brucei*	M, B	EG4, HG4, N4, S3	Ubiquitous (Montenegro et al., 2023)
	Agalmatidae	*Marrus orthocanna*	M, B	EG4, HG4, N4, S3	Arctic-boreal (Stepanjants, 1989)

(Continues)

TABLE 1 (Continued)

Phylum (total no. MOTUs)	Family	MOTU name	Depth zone	Location	Biogeographical distribution
		Hydrozoa_28	All	EG1, EG4, HG4, N4, S3	
	Atollidae	*Atolla tenella*	M, B	EG4, HG4, N4, S3	Arctic (Raskoff et al., 2010)
		Anthoathecata_1	M, B	EG4, HG4, N4, S3	
		Hydrozoa_27	All	EG1, EG4, HG4, N4, S3	
		Mitrocomidae	M, B	HG4, N4, S3	
		Scyphozoa	U-E, L-E, M	EG1, EG4, HG4, N4, S3, SV2	
		Anthozoa_3	U-E, M, B	EG1, EG4, HG4, N4, S3	
		Hydrozoa_26	B	EG4, HG4, N4, S3	
		Hydrozoa_25	M	N4	
		Hydrozoa_24	M, B	EG4, HG4, N4, S3	
		Hydrozoa_22	U-E, L-E, M	EG1, EG4, HG4, N4, S3	
Ctenophora (2)	Bolinopsidae	*Bolinopsis* sp.	L-E, M	HG4, N4, S3	
		Nuda	M	N4	
Echinodermata (9)	Ophiuridae	*Ophiocten gracilis*	U-E, M, B	S3	Arctic-boreal (Degen & Faulwetter, 2019)
	Ophiuridae	*Ophiura robusta*	U-E	SV2	Arctic-boreal (Degen & Faulwetter, 2019)
	Ophiactidae	*Ophiopholis aculeata*	U-E	N4, SV2	Arctic-boreal (Degen & Faulwetter, 2019)
	Pourtalesiidae	*Pourtalesia jeffreysi*	B	HG4	Arctic (Degen & Faulwetter, 2019)
		Echinodermata	All	EG4, HG4, N4, S3	
Mollusca (13)	Hiatellidae	*Hiatella* sp.	M, B	N4	
	Cirroteuthidae	*Cirroteuthis muelleri*	B	EG4, HG4, S3	Arctic-boreal (Xavier et al., 2018)
	Gonatidae	*Gonatus* sp.	M, B	N4, S3	Arctic-boreal (Xavier et al., 2018)
	Gadilidae	*Siphonodentalium lobatum*	M, B	HG4, N4	Arctic-boreal (Degen & Faulwetter, 2019)
		Gastropoda_7	B	EG4, N4, S3	
Porifera (33)		Demospongiae_21	All	EG1, EG4, HG4, N4, S3, SV2	
		Demospongiae_20	All	EG1, EG4, HG4, N4, S3	
		Demospongiae_19	M, B	EG4, HG4, N4, S3	
		Demospongiae_18	U-E, M, B	EG4, HG4, N4, S3, SV2	

TABLE 1 (Continued)

Phylum (total no. MOTUs)	Family	MOTU name	Depth zone	Location	Biogeographical distribution
		Demospongiae_17	U-E, L-E	All	
Rotifera (10)		Monogononta_2	U-E	EG4	
	Euchlanidae	*Euchlanis dilatata*	M, B	EG4, HG4, N4, S3	
		Ploima_6	U-E	EG1, EG4	
		Monogononta_1	B	N4, S3	
		Ploima_5	B	S3	

Note: 15 MOTUs are displayed each for Arthropoda and Cnidaria, five each for the remaining phyla. Details on which sampling location and depth zone each MOTU was detected in are also shown. Depth zones are defined as B, bathypelagic; L-E, lower-epipelagic; M, mesopelagic; U-E, upper-epipelagic. When assigned to species level, the biogeographic origin was listed where possible, with references therein.

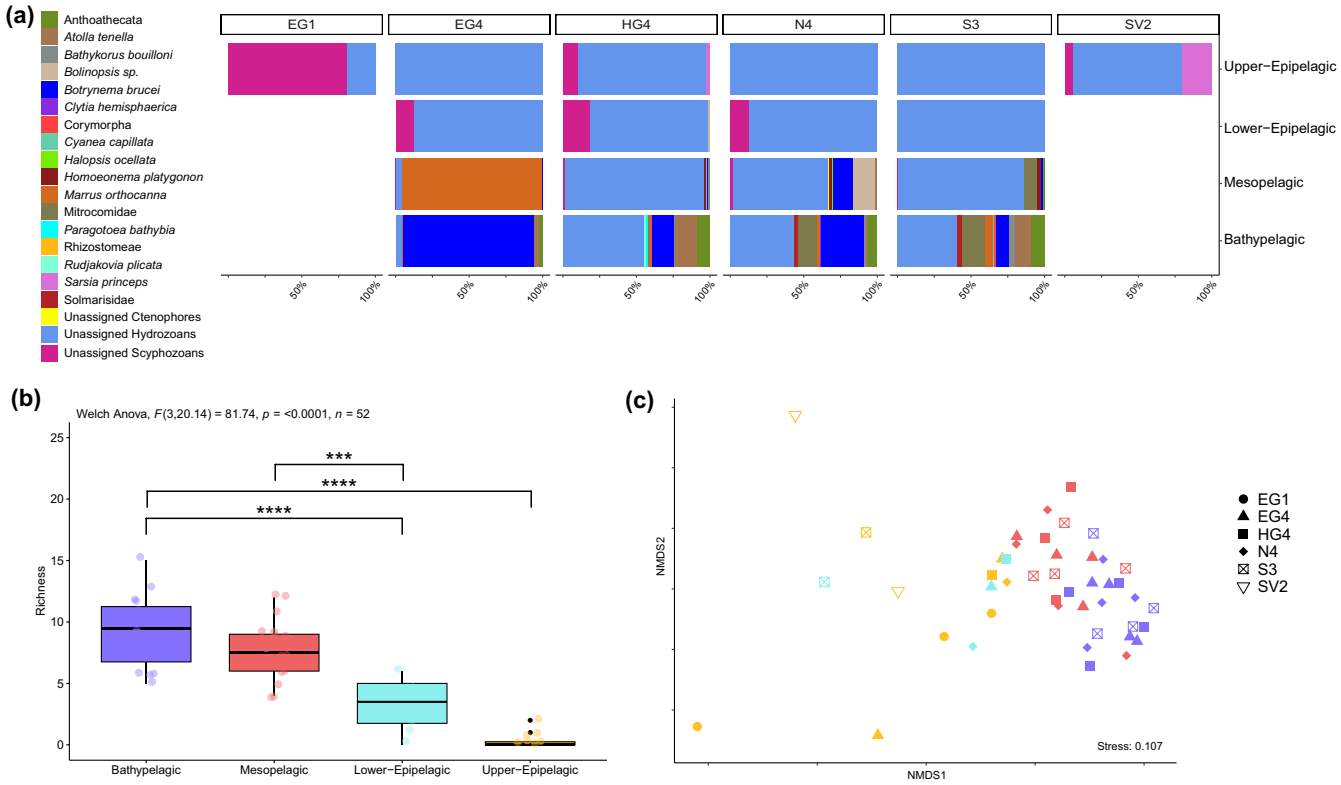

FIGURE 3 Gelatinous zooplankton (GZP) alpha and beta-diversity patterns. (a) Relative read abundances of GZP MOTUs were assigned to >80% for each of the surveyed stations except SV4, where no GZP MOTUs were detected. MOTUs have been pooled by the lowest taxonomic level identified. (b) Species richness was tested with Welch ANOVA on non-rarefied data at the four deep stations. Pairwise comparison with Games-Howell. (c) Nonlinear multidimensional scaling for community structuring of GZP MOTUs ($K=2$). Stress value displayed on plot. Ordination is based on presence-absence data with Jaccard distance. Colors indicate ocean zones, and point shape indicates station, stress value displayed on plot. Depth zones are defined as upper-epipelagic (0–99 m), lower-epipelagic (100–200 m), mesopelagic (201–1000 m), and bathypelagic (>1000 m).

3.4 | Beta diversity and environmental drivers of community composition

We used beta-diversity analysis to test for significant effects of location and depth zone on community composition. For marine metazoans, we identified a significant difference between samples based on depth zone (Figure 2d) (PERMANOVA; $F=7.7276$, $p=0.001$). Further pairwise comparisons indicated that all depth layers were significantly different from each other (*pairwise.adonis*, $p<0.05$; Table S4). Similarly, depth zone was identified as a significant driver of beta diversity in the GZP dataset (Figure 3d) (PERMANOVA; $F=3.9143$, $p=0.001$), with differences between all zones (*pairwise.adonis*, $p<0.05$) except for the upper-epipelagic and lower-epipelagic layers (Table S4). However, this

PERMANOVA result could be affected by the non-homogeneous dispersion detected in the upper-epipelagic zone (*betadisper*, $F = 3.9767$, $p = 0.01413$).

We conducted an sPLS regression analysis to investigate the correlation between MOTUs and environmental conditions (Figure 4). We identified 40 marine metazoan MOTUs that exhibited significant correlations to at least one measured environmental parameter (Pearson's coefficient > 0.4, $p < 0.05$), 11 of which were GZP. The hierarchical clustering suggested that these MOTUs make up three main clusters. The MOTUs in cluster 1 showed strong positive correlations with oxygen saturation, fluorescence, temperature, and longitude, as well as a correlation with shallow sampling depths. These conditions are indicative of surface waters of Atlantic origin near Svalbard. This cluster was largely dominated by copepod MOTUs, including species of the *Oithona*, *Pseudocalanus*, and *Calanus* genera. In contrast, cluster 2 MOTUs exhibited negative correlations with salinity, longitude, and depth, and positive correlations with oxygen saturation, all of which are characteristic of upper ocean polar water masses (PW). This cluster contained hydrozoan and scyphozoan MOTUs as well as the cold-water associated copepod *Microcalanus pygmaeus*. The MOTUs in cluster 3 represented deepwater (DW) residing organisms, indicated by strong positive correlations with depth. This cluster contained the most MOTUs, including the deepwater GZP *Bathykorus bouilloni* and *A.tenella*, as well as the glass sponge *Caulophacus arcticus*.

3.5 | eDNA versus net and optical sampling methods

We set out to compare our metabarcoding results with those obtained from net tows and video surveys for the detection GZP. Both

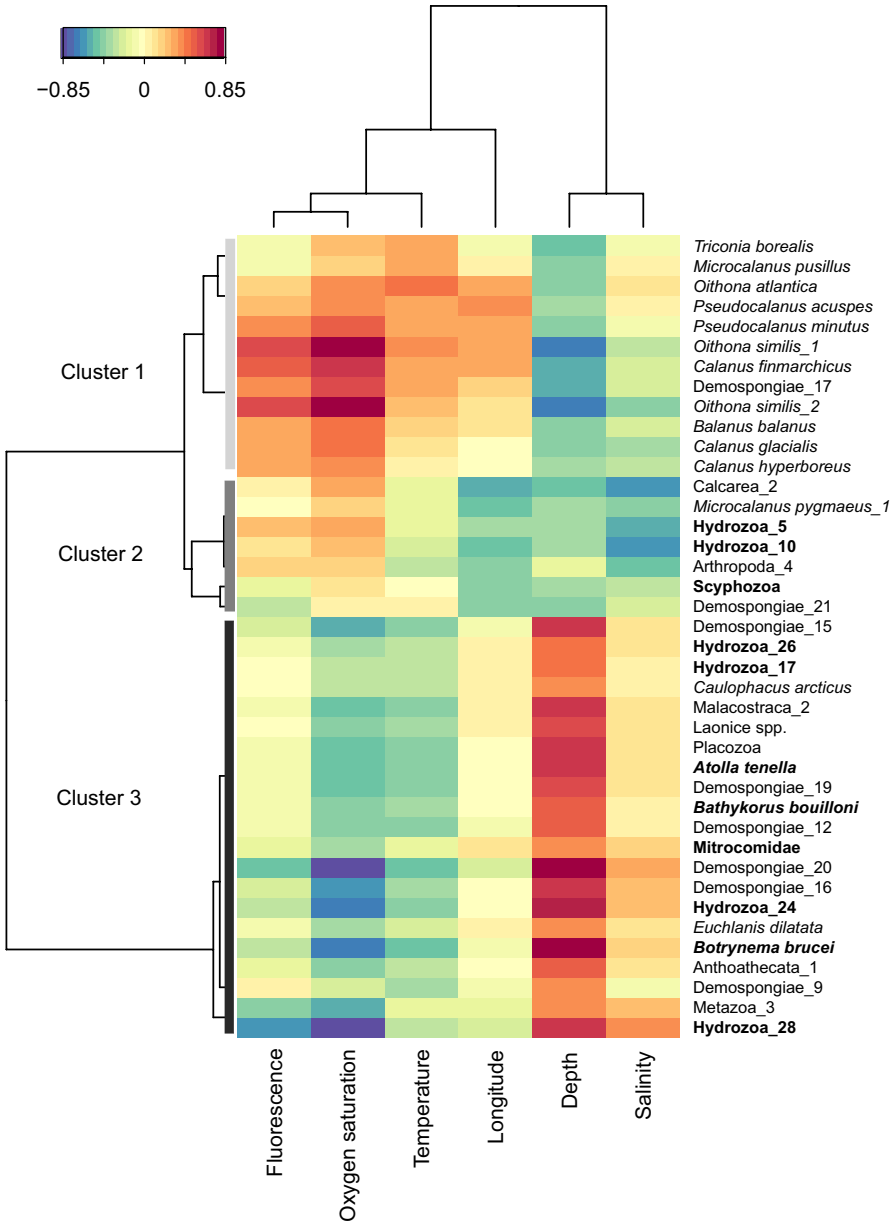

FIGURE 4 A clustered image map (CIM) of three sPLS components with significant pairwise correlations of metazoan MOTU abundance with environmental variables. sPLS clusters on the Y-axis. Correlation cut-off = 0.4. Fluorescence was measured in (mg/m^3), Oxygen saturation in (%), Temperature in degrees Celsius, Longitude in decimal degrees, sample depth in meters, and salinity in (psu). Color indicates correlation type (red = positive and blue = negative) and strength of environmental parameter with a relative abundance of MOTU. Gelatinous zooplankton MOTUs are indicated in bold text.

eDNA and net sampling were undertaken at all seven locations. A total of 22 GZP taxa were detected with eDNA metabarcoding (with MOTUs collapsed into the closest taxonomic match), while net tows detected 19 taxa (Figure 5a). The only overlapping taxon was the hydrozoan species *Sarsia princeps*, which was found at one station (SV2) with nets and at two with eDNA (SV2 and HG4). Although both eDNA and nets detected specimens of the *Botrynema* and *Atolla* genera, species-level identification of net specimens was not possible without further confirmation by molecular barcoding. When comparing the recovery of GZP taxa between the methods at each of the seven stations, eDNA detected an equal or higher number of taxa than nets at each taxonomic level (Figure 5b). The largest differences were at the order level (eDNA $n=13$ vs. nets $n=8$) and the species level (eDNA $n=11$ vs. nets $n=7$). At three stations (EG4, HG4, and S3), three methods were deployed: video transects (PELAGIOS), net, and eDNA sampling. Here, we detected 11 taxa at the genus and species levels (class for ctenophores) with both eDNA and video analyses, while eight taxa were detected in the nets. Three ctenophore taxa (*Beroe* spp., *Bolinopsis* sp., and Cydippida) were detected with the video transects compared to one ctenophore taxon (*Bolinopsis* sp.) detected with eDNA and nets. A higher number of taxa were shared between the nets and video transects ($n=5$) compared to eDNA and video transects ($n=2$). The only taxa detected by all three methods were the *Atolla* and *Botrynema* genera (Figure 5c).

4 | DISCUSSION

As a gateway between the Atlantic Ocean and the Arctic Basin, Fram Strait is a region particularly affected by rapid ecosystem changes. Zooplankton communities, long considered sentinels for biotic and abiotic changes, have already exhibited alterations in species composition, range-shifts, and food web structure in the region, driven by Atlantification (Berry et al., 2019; Csapó et al., 2021). To monitor such changes and their consequences on the wider ecosystem, an increase in biodiversity surveillance is necessary. Metabarcoding of eDNA in water samples is a cost-efficient biodiversity monitoring tool, which is increasingly utilized in marine ecosystems and can help fill knowledge gaps left by traditional monitoring methods. Many studies investigating marine metazoan biodiversity with eDNA have focused on coastal areas and the epipelagic zone, with few targeting mesopelagic and bathypelagic zones or the open ocean (Feng et al., 2022; Govindarajan et al., 2021; Suter et al., 2021). This leaves the vast, deep ocean zones and difficult-to-access areas, such as the Arctic, understudied, particularly with respect to metazoan and GZP diversity (Havermans et al., 2022). In the Arctic, there have been studies using the COI marker to target metazoan biodiversity in coastal areas (Lacoursière-Roussel et al., 2018; Leduc et al., 2019; Nguyen et al., 2023; Sevellec et al., 2021), as well as in the open Chukchi Sea (Questel et al., 2021) and the Pacific Arctic (Ershova et al., 2019). A previous eDNA study has investigated metazoan diversity in Fram Strait, albeit with taxon-specific markers including fish 12S rDNA primers and a primer set targeting cephalopods (Merten et al., 2023). Our study is the first to investigate pelagic metazoan diversity, and specifically GZP diversity, in Fram Strait using the universal metazoan COI metabarcoding marker. Here, we show that eDNA successfully detected a high proportion of the zooplankton community in the area. Furthermore, we characterized marine metazoan and GZP communities by depth zone and revealed significant relationships between taxa and water masses. Lastly, we show that eDNA is an effective and resource-efficient method for increasing GZP detections and enriching traditional biodiversity surveys.

4.1 | Taxonomic composition

Consistent with previous studies in the region, the pelagic community detected by eDNA metabarcoding in our study was made up of a combination of species with different biogeographical distributions. We successfully detected "true" Arctic species (e.g., *C. glacialis*, *Boreogadus saida*, and *B. bouilloni*), as well as arctic-boreal (e.g., *Microcalanus* spp., *Gonatus* sp., and *Pholoe assimilis*) and boreal species (*C. finmarchicus* and *Oithona* spp.) (Table 1). Species known to be highly abundant in Fram Strait were indeed represented by a large number of reads in the eDNA dataset, including the copepods *Calanus hyperboreus*, *C. finmarchicus*, and *Oithona* spp. This is in line with morphological studies in the same area (Darnis & Fortier, 2014; Gluchowska, Dalpadado et al., 2017; Ingvaldsen et al., 2023; Kosobokova et al., 2011), as well as findings in the Chukchi Sea (Questel et al., 2021). We recovered sequences from holoplanktonic (e.g., physonect siphonophores and calanoid copepods) and benthic taxa (e.g., bryozoans and polychaete worms), including many with meroplankton life stages (e.g., echinoderms and poriferans). Benthic taxa are often missed by pelagic sampling techniques, while the pelagic stages of meroplanktonic taxa are commonly sampled with nets but often are difficult to identify based on morphology due to their small size and their lack of easily identifiable features (Descôteaux et al., 2021; Ershova et al., 2019). Furthermore, we detected larger invertebrates (*Cirroteuthis muelleri*) and vertebrates such as the narwhal (*Monodon monoceros*), the bowhead whale (*Balaena mystictus*), and Brünnich's guillemot (*Uria lomvia*). The ability of COI metabarcoding to detect a wide range of marine metazoans at the community and species level has been well-documented in recent years (e.g., Antich et al., 2022; Ershova et al., 2019; Wangensteen et al., 2018). The large taxonomic and size spectrum of organisms detected in the present study further highlights the efficacy of the COI fragment as a marker for detecting the presence of highly mobile, less abundant, and elusive taxa in the Arctic, as well as a range of life strategies that typically require distinct sampling strategies.

Both the marine metazoan sequence reads, and species richness values were dominated by copepods (Calanoida and Cyclopoida) and Hydromedusae taxa (*B. brucei* and *M. orthocanna*). While the reads showed expected relationships between read abundances of highly abundant taxa (i.e., in *Calanus* copepods), further quantitative interpretations related to abundance or biomass must be made with

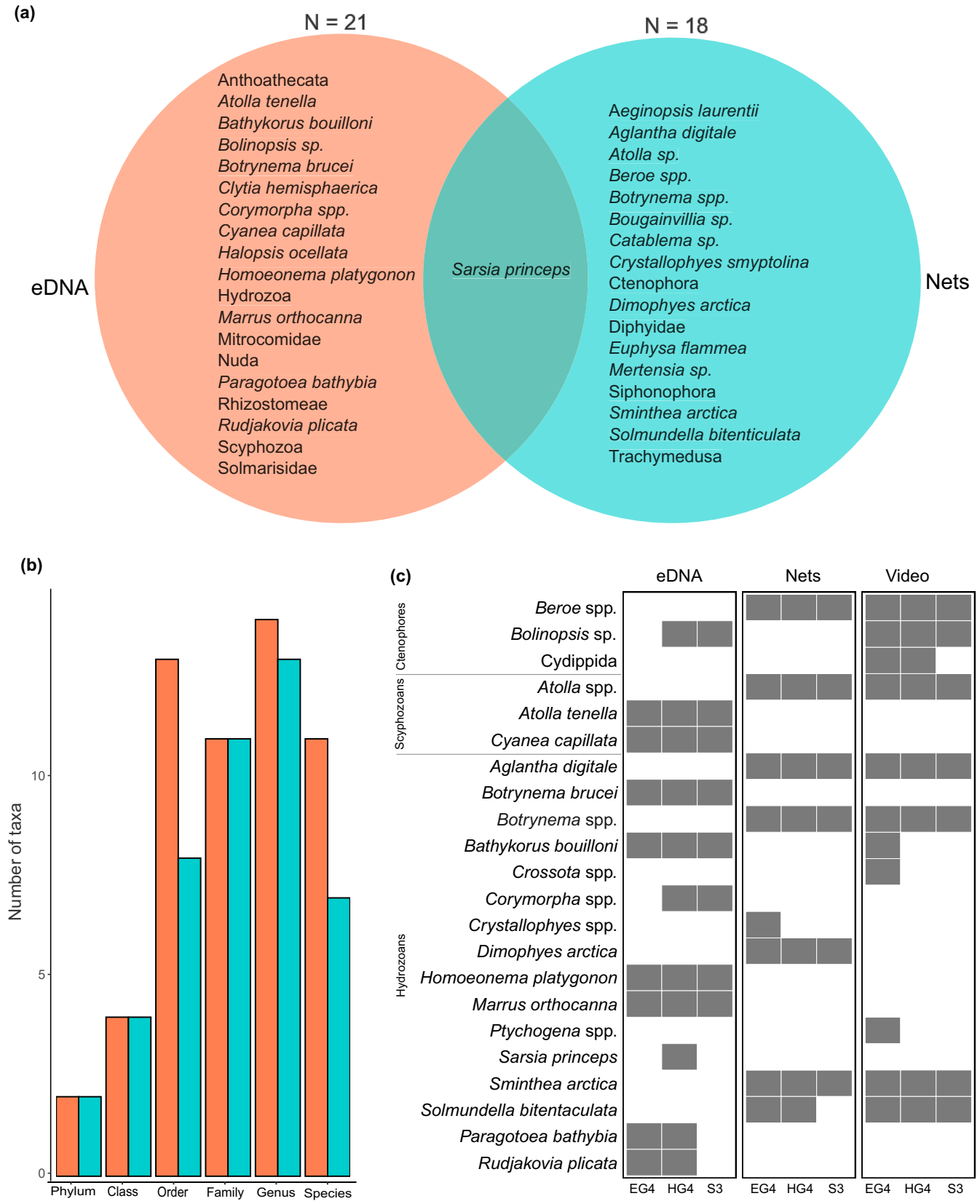

FIGURE 5 Comparisons between eDNA metabarcoding results and net and video sampling methods. (a) The number of taxa detected by eDNA and nets across all of the seven sampling locations combined. MOTUs are collapsed into the closest taxonomic level. (b) The number of taxa detected at each taxonomic level from presence data detected by nets and eDNA from all of the seven sampling locations combined. (c) Shows the class (ctenophores only), genus, and species-level detections at the three stations where eDNA, nets, and video surveys were conducted (EG4, HG4, and S3). Gray squares indicate the presence of a taxa.

caution. Positive relationships between sequence reads and biomass have been found for a number of zooplankton taxa (Ershova et al., 2023), and specifically copepods (Ershova et al., 2021) when metabarcoding bulk samples. However, factors including the different nature of extra-cellular DNA versus bulk samples, PCR biases (Lacoursière-Roussel et al., 2018; Wangensteen et al., 2018) and taxon-specific knowledge gaps (Bucklin et al., 2010) still limit the use of eDNA metabarcoding to draw these conclusions on a community-wide scale. It is noteworthy that we had low read abundances or failed to detect zooplankton taxa that are commonly caught in net and optical surveys in the Arctic. For example, we obtained low read numbers and MOTU richness for Malacostraca (e.g., *Thysanoessa inermis*, *T. longicaudata*, and *Themisto libellula*), which are typically characterized by high biomass in the Arctic seas (Eriksen et al., 2017; Kosobokova et al., 2011). These false negatives could have multiple explanations, where primer and PCR biases as well as underrepresentation on public databases (e.g., appendicularians and the ctenophore *Mertensia ovum*), appear most likely. Furthermore, the COI Leray fragment may be an unsuitable barcode region for certain zooplankton taxa (Bucklin et al., 2021), although here we applied the modified Leray-XT primer, which has improved coverage of some marine taxa than the original (Wangensteen et al., 2018). Nevertheless, the inclusion of additional markers such as 18S regions or group-specific primers could help to resolve these omissions. Moreover, reasons such as taxon-specific eDNA shedding rates, higher degradation rates (Andruszkiewicz Allan et al., 2021), or the limited sampling volume of seawater cannot be excluded.

4.2 | Vertical patterns of diversity

Epipelagic waters in the Arctic are typically dominated by a low number of zooplankton species, mainly *Calanus* copepods, which exhibit high biomass and abundance (Gluchowska, Trudnowska et al., 2017; Hop et al., 2019). This was reflected in our eDNA results, wherein epipelagic layers were characterized by a low diversity and dominated by Arthropoda. Alpha diversity increased in the mesopelagic and bathypelagic layers, where the contributions of other phyla such as cnidarians and poriferans increased both in reads and taxa richness. Multivariate analysis of community composition showed the greatest differences between the epipelagic and the bathypelagic assemblages in both datasets. These vertical patterns are consistent with findings of net-based zooplankton studies in the Arctic, which have shown similar results of diversity peaking in the mesopelagic or deeper, despite a decrease in overall biomass (Gluchowska, Trudnowska et al., 2017; Kosobokova et al., 2011). It also corroborates previous eDNA results on fish in Fram Strait, showing a maximum species richness in the bathypelagic zone (Merten et al., 2023).

We detected clear vertical gradients in diversity and relative read abundances for GZP. Both diversity and relative abundances increased from epi- to meso- and bathypelagic layers, where, at one station, GZP were present in higher proportions than Arthropoda (Figure 2a). These vertical patterns reflect previous findings from Fram Strait (Gluchowska, Trudnowska et al., 2017; Mańko et al., 2020; Pantiukhin et al., 2023a) and other Arctic regions (Kosobokova et al., 2011; Raskoff et al., 2010). For instance, Raskoff et al. (2010) reported higher species richness in the meso- and bathypelagic layers, dominated by medusae, in the Canada Basin and Chukchi Plateau, with reduced diversity but increased numbers of ctenophores and siphonophores in shallower layers. An optical survey with the PELAGIOS video system, conducted during the same expedition as the present study, also resulted in depth being identified as a significant driver of GZP diversity and distribution (Pantiukhin et al., 2023a), with peak diversity detected at 1200 m. Furthermore, eDNA zooplankton surveys in the open ocean have also found the diversity of GZP to increase with depth (Feng et al., 2022; Govindarajan et al., 2021), indicating that eDNA metabarcoding of the COI gene enables the accurate detection of vertical diversity gradients. Although the overall patterns of vertical diversity observed in this study are in line with those previously reported from Fram Strait, it is important to acknowledge that factors, including sampling time and filter choice, as well as a degree of uncertainty regarding the source of eDNA signals, can impact the results. For instance, high levels of biological activity in Arctic surface waters during summer due to phytoplankton blooms and seasonal vertical migration of zooplankton (Norrbin et al., 2009) result in elevated levels of particles suspended in the water column. Under such conditions, the use of small pore-size membrane filters, as was the case here, increases the susceptibility of clogging compared to large pore-size membrane filters (Kumar et al., 2022; Singer et al., 2019), resulting in potentially lower observed diversity in the epipelagic layer. The persistence of eDNA may also affect patterns observed, with eDNA signals being potentially advected or remaining detectable for extended periods. However, Suter et al., 2021 were able to detect diel migration patterns in copepods, indicating that the eDNA was detected when the organisms were present. This and other recent findings suggest that eDNA is potentially diluted or degraded more rapidly in marine environments than in experimental conditions (e.g., Jeunen et al., 2019). The significantly higher alpha diversity observed in the bathypelagic may in part be explained by the fact that eDNA is typically preserved in higher quality and concentrations in sediment than water (Holman et al., 2019; Ogata et al., 2021; Sakata et al., 2020). Disturbances in sediment may lead to eDNA being resuspended in the demersal layer. We cannot exclude that these factors may have impacted the patterns of metazoan diversity observed in the present study. Although eDNA metabarcoding has known limitations relating to the identification of sequences, with the common issue of unassigned MOTUs (Berry et al., 2019), alpha and beta-diversity analyses are independent of taxon information and therefore prove valuable insights into biodiversity and community composition. Taxa with lower matches in databases still provide valuable information pertaining to patterns of diversity. We highlight the need for more eDNA surveys in deeper areas, increasing water volume filtered and the number of sampling points throughout the water column to allow for higher taxonomic and depth resolution.

4.3 | Water mass indicators as drivers of community composition

The role of water masses as drivers of Arctic zooplankton distribution and community composition is well documented for Fram Strait based on net-based surveys (e.g., Basedow et al., 2018; Gluchowska, Dalpadado et al., 2017; Hop et al., 2019) and sediment traps (e.g., Ramondenc et al., 2023; Schröter et al., 2019). Similar patterns have also been shown for GZP, based both on net and optical surveys (Mańko et al., 2020, 2022; Pantiukhin et al., 2023a). In an eDNA study based on sediment samples, the influence of AW masses was found to be a significant driver of foraminifera community composition in Svalbard fjords (Nguyen et al., 2023). Through sparse partial least squares regression analysis (sPLS), our dataset revealed well-documented relationships between marine Metazoa and environmental variables, as well as associations that may point to previously unknown indicator taxa. These associations were most numerous in the copepod fraction of the zooplankton community. For example, the highly abundant and herbivorous Atlantic expatriate, *C. finmarchicus*, showed strong correlations with shallow depths, high oxygen and fluorescence values, indicating associations with phytoplankton bloom conditions. It also correlated with warmer temperatures and higher salinity, which are characteristics of AW masses. *Oithona atlantica* also showed significant correlations with AW mass characteristics as well as eastern longitudes, indicating a positive relationship with the Atlantic-influenced central Fram Strait and Svalbard stations. The increase of Atlantic *C. finmarchicus* and *Oithona* species is considered a signal of the progressing Atlantification in Fram Strait (Gluchowska, Dalpadado et al., 2017). In contrast, *M. pygmaeus*, a cold-water associated species (Søreide et al., 2022), was significantly correlated with PW conditions of the East Greenland slope (low salinity, high oxygen), where it was found in high read numbers in the upper-epipelagic layer. Similar correlations were also observed for *Calanus glacialis* and *C. hyperboreus*, which have both been previously recognized as indicator species of PW masses (Gluchowska, Trudnowska et al., 2017; Svensen et al., 2011). Neither species showed strong correlations with temperature; however, higher sampling resolution across wider environmental gradients would likely improve the analysis.

Within the GZP community, we found correlations between eDNA read counts and environmental parameters that are in line with existing ecological knowledge of the species. *B. bouilloni*, *B. brucei*, and *A. tenella* were correlated with conditions of deepwater masses. This is in agreement with their detection in deep waters in Fram Strait using video surveys (Pantiukhin et al., 2023a) as well as findings from other Arctic regions (Raskoff, 2010; Raskoff et al., 2010). However, while Pantiukhin et al. (2023a) did not find a major effect of salinity on GZP community composition in Fram Strait, we found significant associations with higher salinity in the deepwater cluster and lower salinity in cluster 2 (the MOTUs named Hydrozoa_5, Hydrozoa_10 and Scyphozoa). Interestingly, we found significant negative correlations of the same three MOTUs with longitude despite finding no significant influence of sampling location on community composition, suggesting an affinity to PW and the western side of Fram Strait.

The fact that we were able to detect well-known water mass associations of highly abundant copepod species and less abundant deepwater species such as *B. bouilloni*, highlights the strength of our approach for capturing zooplankton and, more specifically, GZP dynamics. Although conclusions from our sPLS analysis are somewhat hindered by the ability to taxonomically resolve MOTUs and the lack of knowledge about the ecology of detected taxa, it serves as a valuable approach for identifying potential indicator species associated with distinct conditions and as a means to generate hypotheses. Such hypotheses can be tested through increased resolution of eDNA sampling, especially in the understudied mesopelagic layers of the Arctic, in connection with net- and camera-based investigations. Therefore, this study shows the potential of eDNA as a cost- and time-effective tool for not only detecting pelagic Arctic diversity but also for monitoring shifts in Arctic zooplankton communities in the context of climate change-induced perturbations.

4.4 | eDNA as a tool to improve gelatinous zooplankton surveys

Gelatinous zooplankton are elusive and are notoriously difficult to catch in good condition. They are easily destroyed in typical zooplankton nets and other trawling gear. There are known sampling biases between types of trawls and nets (Nogueira Júnior et al., 2015), and while optical methods can detect individuals without destroying them, they also have known biases that can affect species composition results (Hosia et al., 2017). Even when detected or caught in good condition, GZP can also be difficult to identify morphologically without expert knowledge. Due to these challenges, GZP is regularly underestimated in terms of diversity, distribution, and abundance (Govindarajan et al., 2021; Hosia et al., 2017; Long et al., 2021). The implementation of eDNA for surveying GZP biodiversity has been integrated within broader assessments of marine biodiversity, including zooplankton in coral reefs in Florida (Djurhuus et al., 2018), as a part of a mesozooplankton survey in the Western Pacific (Feng et al., 2022) and in the mesopelagic zone in the North-Atlantic (Govindarajan et al., 2021). Studies with a focus on single-species GZP detection have been increasing in number in temperate and tropical areas including scyphozoan species in the Sea of Japan (Minamoto et al., 2017; Ogata et al., 2021; Takasu et al., 2019), and cubozoans (Bolte et al., 2021; Morrissey et al., 2022). However, the use of eDNA metabarcoding studies truly focused on jellyfish biodiversity and at the community level are limited. Jellyfish blooms can have major top-down ecosystem impacts on local and regional scales (Zagorodnyaya et al., 2023), on fisheries stocks and tourism (Bosch-Belmar et al., 2020; Ruiz-Frau, 2022). An increase in GZP abundances with further climate change has been projected for Fram Strait, concomitant with a decrease in diversity (Pantiukhin et al., 2023a). There is a need for cost-efficient monitoring tools

to track and further understand their community composition and abundance and implement mitigation strategies where necessary or make accurate future predictions.

Our results demonstrated that the GZP community composition detected is strongly influenced by the sampling methodology used. When comparing methods at the genus and species level, all three methods detected similar numbers of taxa, albeit with pronounced differences in composition (Figure 5a). When comparing eDNA with net catches, eDNA recovered more taxa overall, with nearly double the taxa at the order level (Figure 5b). Our results are consistent with several other studies that targeted open-ocean zooplankton communities and compared eDNA metabarcoding and net sampling. For example, Feng et al. (2022) and Govindarajan et al. (2021) both found two to four times as many medusae taxa with eDNA sampling compared to net tows. Given that all three sampling methods were conducted within hours of each other, it is unlikely that temporal shifts in the community composition of GZP are the reason for these differences. Thus, the differences are likely a consequence of varying sampling strategies, identification expertise, and underrepresentation of taxa on public barcode databases. The coverage and deployment of the three sampling strategies in this study are distinct in both the amount of water covered and their spatial dimensions. Water for eDNA sampling was taken at discrete depths on vertical CTD haul with a maximum sampling volume of 6 L at each sampling event. In contrast, nets were either hauled vertically or with oblique tows behind the ship, covering large sections of the water column. The video transects were carried out as horizontal transects at specific depths, also surveying thousands of liters of water (Pantiukhin et al., 2023a). Despite this, the eDNA study recovered the highest number of species-level detections.

An advantage of eDNA is that it can circumvent the likelihood of delicate and small specimens being destroyed or remaining undetected in net sampling, as well as the escape reactions of larger taxa (Andruszkiewicz Allan et al., 2021; Minamoto et al., 2017). Moreover, GZP has seemingly high DNA-shedding rates, increasing the likelihood of detection with eDNA (Andruszkiewicz Allan et al., 2021). Video surveys have the advantage of being able to detect different life stages, allow for abundance estimates and avoid damaging specimens like nets do. However, identifications to a lower taxonomic level may be hampered by image quality and the lack of molecular samples to reliably differentiate closely related or cryptic species (Montenegro et al., 2023). Issues with accurate morphological identifications have been highlighted for several GZP taxa recovered by nets and videos in Fram Strait. These include the distinction between species in the *Atolla* genus (Matsumoto et al., 2022), the narcomedusae *Aeginopsis laurentii* which is thought to have been historically confused with the recently described *B. bouilloni* (Raskoff, 2010), and the distinct bell shape used as the main identifier between *B. brucei* and *B. ellinorae* (Montenegro et al., 2023). Based on the eDNA results, we detected *A. tenella*, *B. bouilloni*, and *B. brucei* with 100% sequence identity matches. Furthermore, the species diversity of ctenophores is particularly poorly resolved in the Arctic (Majaneva & Majaneva, 2013).

Despite the many advantages, remaining limitations to eDNA metabarcoding prevent it from being a stand-alone survey method for capturing the entire GZP community. For example, we did not detect the hydrozoan species *A. digitale*, *S. arctica* and *Dimophyes arctica*, all of which are highly abundant in the area, as demonstrated by both the net and video surveys (Havermans et al., 2021; Pantiukhin et al., 2023a). All three of these GZP species are posited to be heavily influenced in the future by warming in the Arctic (Mańko et al., 2020, 2022; Pantiukhin et al., 2023a). Further omissions include reads assigned to the ctenophore *M. ovum* and appendicularians, both of which are particularly abundant components of the GZP community in Arctic surface waters (Gluchowska, Dalpadado et al., 2017; Raskoff et al., 2010), including Fram Strait (Havermans et al., 2021; Mańko et al., 2020). A number of GZP taxa known to occur in Fram Strait are poorly represented on public databases, severely hindering the ability of eDNA to detect them, with some having few available sequences (e.g., *Crystallophyes* sp.) and others with sequences only from other oceans (e.g., *D. arctica*). The highly abundant hydrozoan *S. arctica* has no publicly available COI barcodes on NCBI nor BOLD and has been categorized as "taxon inquirendum" in the WoRMs database (WoRMS Editorial Board, 2023). There are also no verified species-level barcode records of the Narcomedusae family Solmarisidae (detected here with eDNA). Additionally, taxa in the highly abundant Diphyidae family, known as bullet-shaped siphonophores, are difficult to identify morphologically due to their tendency to be damaged in nets and fixation by ethanol (Park et al., 2021). For example, D. *arctica* is often confused with *Muggiaea bargmannae* (Mańko et al., 2020) yet there are no publicly available COI sequences on BOLD for *M. bargmannae*, limiting our ability to further distinguish them with (meta)barcoding. With more than half of GZP MOTUs herein being identified only to class level, an increase in barcoding effort for GZP, and particularly hydrozoans, would no doubt increase our eDNA species list as well as improve the accuracy and taxonomic resolution of net detections. Furthermore, future research should include in silico PCRs to identify potential primer mismatches in GZP taxa, the impact of which on the current study cannot be ruled out.

5 | CONCLUSIONS

We demonstrated the use of eDNA metabarcoding as a successful and efficient method to complement the current biodiversity monitoring of pelagic metazoans in the Arctic Ocean and hereby provide the first GZP-focused eDNA metabarcoding biodiversity assessment in the Arctic. Our survey showed that it is possible to recover diversity patterns at a broad scale for the metazoan community as well as at a higher resolution with a targeted group of taxa using the COI barcode. Furthermore, we demonstrated that with only a single marker, a higher number of unique GZP taxa could be recovered from only a small amount of water compared to long net tows and video transects at the same locations. We propose eDNA as a supplementary tool to current biodiversity methods, both for metazoans and GZP,

rather than a replacement. As standardization improves and current limitations are overcome, for example, increased barcoding efforts to improve reference databases, the opportunity to use eDNA to detect and track changes in biodiversity across marine ecosystems will expand. Further analysis of community patterns, as well as crucial species-level information such as indicator species and rare and invasive taxa, will increase understanding of known shifts in marine communities, as well as validate predicted future scenarios in the Arctic.

AUTHOR CONTRIBUTIONS

CH conceived the study and, together with AM, developed the study design. CH planned the field work and collected the samples. AM conducted the laboratory work. AM analyzed the data, with contributions from TP, AA, WVA, and SN. AM wrote the manuscript with revisions by CH. CH acquired the funding resources. All authors contributed by revising the manuscript and approving the submitted version.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The raw metabarcoding sequencing data from this project are publicly available at NCBI on the SRA database under the BioProject ID: PRJNA1044054. The oceanographic data is publicly available on the Pangea repository https://doi.pangaea.de/10.1594/PANGAEA.940754.

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