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RESEARCH ARTICLE

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Distinct latitudinal community patterns of Arctic marine vertebrates along the East Greenlandic coast detected by environmental DNA

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Abstract

Aim: Greenland is one of the places on Earth where the effects of climate change are most evident. The retreat of sea ice has made East Greenland more accessible for longer periods during the year. East Greenland fjords have been notoriously difficult to study due to their remoteness, dense sea ice conditions and lack of infrastructure. As a result, biological monitoring across latitudinal gradients is scarce in East Greenland and relies on sporadic research cruises and trawl data from commercial vessels. We here aim to investigate the transition in fish and marine mammal communities from South to Northeast Greenland using environmental DNA (eDNA).

Location: South to Northeast Greenland.

Methods: We investigated the transition in fish and marine mammal communities from South to Northeast Greenland using eDNA metabarcoding of seawater samples. We included both surface and mesopelagic samples, collected over approximately 2400 km waterway distance, by sampling from Cape Farewell to Ella Island in August 2021.

Results: We demonstrate a clear transition in biological communities from south to northeast, with detected fish and mammal species matching known distributions. Samples from the southern areas were dominated by capelin (*Mallotus villosus*) and redfish (*Sebastes*), whereas northeastern samples were dominated by polar cod (*Boreogadus saida*), sculpins (*Myoxocephalus*) and ringed seal (*Pusa hispida*). We provide newly generated 12S rRNA barcodes from 87 fish species, bringing the public DNA database closer to full taxonomic coverage for Greenlandic fish species for this locus.

Main Conclusions: Our results demonstrate that eDNA sampling can detect latitudinal shifts in marine biological communities of the Arctic region, which can supplement traditional fish surveys in understanding species distributions and community compositions of marine vertebrates. Importantly, sampling of eDNA can be a feasible

approach for detecting northward range expansions in remote areas as climate change progresses.

KEYWORDS
biomonitoring, climate change, fish diversity, fjord systems, latitudinal gradient, polar regions

1 | INTRODUCTION

Greenland is the largest island in the world (excluding continental landmasses) with more than 44,000 km of coastline and a subarctic to high arctic climate. Greenland also encapsulates the second largest ice sheet, only surpassed by the Antarctic ice sheet. With nearly 56,000 inhabitants, Greenland is sparsely populated. This is particularly true for the east coast, where only two small towns (Tasiilaq and Ittoqqortoormiit) and a few settlements currently exist. The Greenlandic coastline is transversed by numerous fjords, among others the longest fjord in the world (Scoresby Sound). The biological communities found in these areas are, with a few exceptions, poorly known due to their geographic inaccessibility (Ghigliotti et al., 2004; Rysgaard et al., 1999). Large differences in community compositions are found across regions, with prominent barriers at the Canada-Greenland and Greenland-Iceland submerged ridges, especially for deep-water biota (Møller et al., 2010).

The consequences of climate change in the Arctic have been widely debated, spurring a massive influx of capital into studying and understanding changes in melting ice sheets, retreating sea ice, ocean freshening and warming of the oceans (AMAP, 2021; Carmack et al., 2016; Wassmann et al., 2020). These geophysical changes are likely to have massive effects on the biological communities, potentially driving range shifts and altering suitable habitats for many species (Heide-Jørgensen et al., 2022; Wisz et al., 2015).

The vast water masses off the Greenland coast have enabled large-scale fisheries, currently constituting >90% of Greenland's national export value (Post et al., 2021). As the Greenlandic economy is heavily dependent on commercial fisheries, several examples of overexploitation and changes in habitat suitability have already been documented, most notably the collapse of the West Greenland Atlantic cod (*Gadus morhua*) in the 1970s (Bonanomi et al., 2015; Rätz, 1999). West and Southeast Greenland offshore waters are surveyed annually by bottom trawl surveys conducted by the Greenland Institute of Natural Resources (GINR) and the German Federal Research Centre for Fisheries. The survey catch data are primarily used for annual stock assessments of commercial species like Atlantic cod, Greenland halibut (*Reinhardtius hippoglossoides*), redfish (*Sebastes*) and northern shrimp (*Pandalus borealis*). Coastal gill-net surveys for Atlantic cod and Greenland halibut are also conducted, and in recent years, pelagic surveys for capelin (*Mallotus villosus*) and mackerel (*Scomber scombrus*) have also been carried out along the east coast. Biological data from Northeast Greenland fjords that are not targeted by fisheries is scarce, and the only recent data that exist from the area have been collected by the TUNU program, which has conducted bottom trawl sampling sporadically since 2002 (Christiansen, 2012; Christiansen et al., 2016, 2021). There is currently very little information on the fisheries' impact on bycaught vertebrate species, as well as on the distribution and abundance of populations of noncommercial vertebrate species. Nevertheless, emerging evidence suggests that population abundance and size-at-maturity declines of bycaught fish species correlate with increased fishing (Hedeholm et al., 2019; Jørgensen et al., 2014). Since conventional bottom trawl surveys are invasive and largely focused on areas of commercial interest, there is a need for less invasive monitoring tools of Greenlandic fish fauna across larger spatial scales, as species are shifting northwards (Christiansen et al., 2014).

Environmental DNA (eDNA) is increasingly used for monitoring marine environments (Berry et al., 2019; Thomsen et al., 2012) and has in recent years expanded to large-scale biogeographic inferences in marine research (Agersnap et al., 2022; Fraija-Fernández et al., 2020; West et al., 2021). Environmental DNA is noninvasive and may be particularly useful in remote areas where data on species occurrence is deficient. For eDNA research to live up to its full potential, inventories of genetic databases such as the National Center for Biotechnology Information (NCBI)'s GenBank must strive for complete taxonomic coverage of at least local species. Focus should be placed not only on commercially important species but also on bycaught, rare and cryptic species, which are all affected by anthropogenic activities. These largely unmonitored species could potentially provide insights into how communities respond to climate change in the Arctic. Establishing molecular-based monitoring tools in addition to conventional fishery surveys should therefore be a priority for detecting temporal dynamics in a changing Arctic.

We here aim to elucidate the current vertebrate communities in East Greenland fjords by using eDNA metabarcoding of seawater samples taken from both surface and mesopelagic waters along a south-to-northeast latitudinal gradient. We also establish a near-complete genetic reference library for fishes to facilitate the future monitoring of the Greenlandic fish fauna through eDNA.

2 | METHODS

2.1 | Sample collection and DNA extraction

Samples were collected on board a Danish navy vessel (*I/F Knud Rasmussen*) on a three-week research cruise from Nuuk to Ella Island from 10 to 26 August 2021 (stations spanning ~2400 km waterway distance from 60°N to 73°N and 48°W to 22°W; Figure 1).

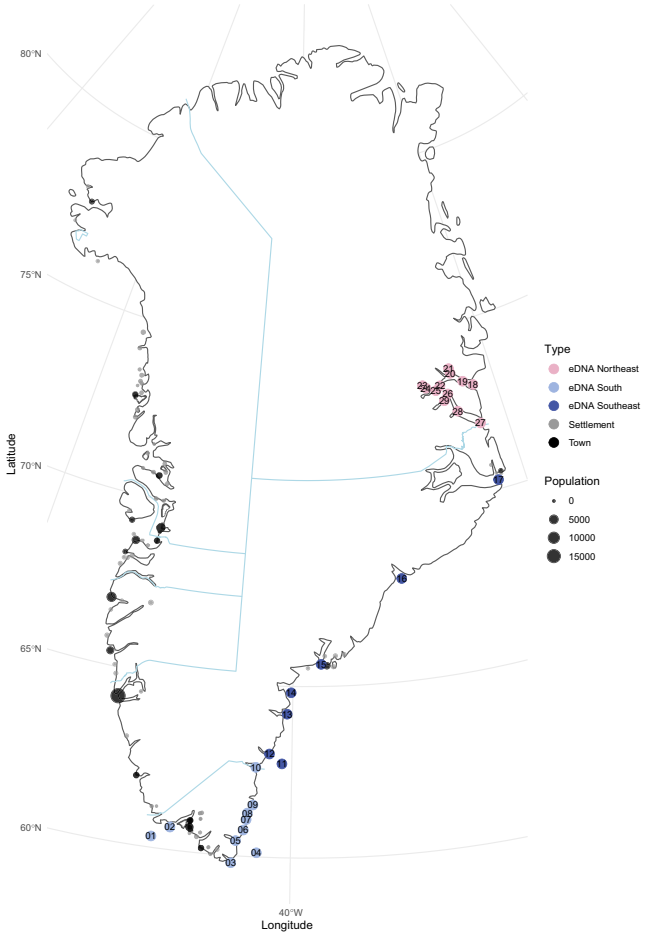

FIGURE 1 Map of Greenland with numbers of human inhabitants in towns (black) and settlements (grey) to illustrate how sparsely populated the sampled areas are. Blue lines define administrative Greenlandic counties (from top left and down: Avannata, Qeqertalik, Qeqqata, Sermersooq, Kujalleq) and the Northeast Greenland National Park (top right). Human inhabitant data are from 1 January 2020 and was downloaded from StatBank Greenland (https://bank.stat.gl/BEEST4; Statbank Greenland, 2020). Numbered circles denote eDNA sampling stations in South (light blue), Southeast (dark blue) and Northeast (pink) Greenland. All eDNA sampling was conducted on a south-northeast research cruise in August 2021.

We initiated sampling in Southern Greenland west of Cape Farewell and opportunistically sampled the fjord systems from Cape Farewell to Ella Island in East Greenland with a total of 29 stations. At each station, standard oceanographic measurements (CTD) were performed as in Rysgaard et al. (2020) (Table 1). We sampled two 1.5 L seawater samples from the surface waters and two 1.5 L seawater samples from deeper, primarily mesopelagic waters (128–509 m depth). In general, we aimed for sampling just above the seabed for the deep samples but were not able to sample deeper than ~500 m due to logistical constraints (Figure S1). In total, we collected 58 surface samples and 56 deeper samples as swells made one deep station impossible. Surface waters were sampled using a weighed-down 10 L bucket and filtered immediately onsite. For the deeper samples, we attached a 5 L Niskin bottle just above the CTD and emptied the Niskin bottle into the same bucket. Similarly, the deep samples were filtered immediately after sampling. Between each sampling event, the bucket was first rinsed with shipboard-produced freshwater (reverse osmosis system) and then rinsed using the first litre of water from the deep samples from the Niskin bottle or by dropping the bucket in the ocean for surface samples. Each water sample was filtered through sterile 0.22 µm Sterivex-GP filters (Merck Life Science, Søborg, Denmark) using 200 mL Soft-Ject syringes (HSW, VWR International), which were refilled seven times to accommodate the 1.5 L of water per sample. All handling of samples was done using sterile gloves and facemasks. Samples were stored in a −18°C freezer immediately after filtering and kept frozen until the DNA extraction in the laboratory. We also collected field blanks and bucket blanks throughout the cruise, to monitor organismal DNA present in the surroundings. Field blanks (n = 4) represent bottled mineral water (0.5 L) brought from Denmark, directly filtered through Sterivex filters. Bucket blanks (n = 2) represent bottled mineral water (0.5 L), which was emptied into the bucket, thus simulating the sampling procedure of any other real sample. The vessel used for sampling is not capable of fish trawling, and to our knowledge, there has been no processing of fish catches on board the vessel. This should alleviate most of the potential contamination sources, and by including negative controls, we are able to keep track of any DNA signal arising from water previously inside the bucket.

DNA was extracted in a clean laboratory facility dedicated to low-concentration samples at the Department of Biology, Aarhus University. DNA was extracted using the DNeasy® Blood & Tissue kit (Qiagen, Cat. no. 69506), applying four times more ATL buffer and proteinase K compared with the manufacturer's protocol and an incubation time of 2 h. We deviated slightly from the manufacturer's protocol by including a bead-beating step for mechanical cell disruption prior to the extraction. During the final extraction step, the spin column was incubated with elution buffer (AE) over two rounds of 37°C for 10 min for a final volume of 120 µL (2*60 µL) (Sigsgaard, Nielsen, Bach, et al., 2017). For each round of extraction, we also included an extraction blank (n = 13), and all extracted samples were stored at −20°C until running PCRs.

2.2 | PCR amplification of eDNA samples

We divided the samples into three separate PCR runs with four replicate PCRs for each run. Each PCR run contained extractions from 37–39 water samples, 1–2 field blanks, 0–2 bucket blanks, 4–5 extraction blanks and 4 PCR blanks. To obtain PCR replicates, we ran each of these PCR runs four times (e.g. run1.1, run1.2, run1.3 and run1.4, with a total of 12 libraries across the three PCR runs). Within each PCR run, every sample was amplified using a mixture of two different primer sets targeting the mitochondrial 12S rRNA gene. We used forward primers Elas02_F (5'-GTTGGTHAATCTCGTGCCAGC-3′) and Tele02_F (5'-AAACTCGTGCCAGCCACC-3′) and reverse

TABLE 1 Overview of sea surface temperatures (SST) and sea surface salinity (SSS), deep water temperatures (DWT) and deep water salinity (DWS) at each station where eDNA samples were collected. DWT and DWS refers to the temperature and salinity measured at the depth at which the "deep sample" from each station was collected (deep sample depth, DSD). Actual depths at sites are listed as "Depth"; see also Figure S1, Supp. Info. All temperatures are measured in °C and salinity in psu. Note that no CTD measurements were made at station 4.

	South									
Station	**01**	**02**	**03**	**04**	**05**	**06**	**07**	**08**	**09**	**10**
SST	2.8	3.9	4.7	-	7.0	5.9	5.5	5.4	4.8	4.4
SSS	32.4	31.9	29.9	-	27.2	25.2	26.2	26.3	26.2	22.5
DWT	5.2	1.1	2.0	-	3.9	3.1	4.1	3.1	3.7	3.9
DWS	34.8	32.3	33.7	-	34.6	34.4	34.6	34.3	34.5	34.6
DSD	234	128.7	137.6	-	443.2	291.9	494.5	497.5	309.7	476.7
Depth	458	150	156	1017	480	305	572	684	354	782

	Southeast						
Station	**11**	**12**	**13**	**14**	**15**	**16**	**17**
SST	7.6	5.1	4.3	4.3	4.3	2.0	3.2
SSS	32.9	24.2	28.2	29.7	28.6	29.4	30.4
DWT	4.6	2.9	4.5	3.8	3.5	1.3	1.0
DWS	34.8	34.4	33.0	34.7	34.6	34.8	34.9
DSD	501.4	496.5	498.5	412.5	501.4	505.4	499.4
Depth	535	674	534	436	910	533	526

	Northeast											
Station	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**
SST	7.6	6.3	6.8	6.7	8.1	6.3	7.1	8.3	9.2	7.9	8.9	9.6
SSS	28.4	28.2	27.2	26.5	24.7	25.0	24.8	25.3	25.4	29.3	24.7	24.8
DWT	1.0	1.1	0.8	−0.2	0.8	1.0	1.0	0.9	0.5	0.7	1.0	0.9
DWS	34.7	34.8	34.7	34.2	34.6	34.6	34.7	34.6	34.5	34.6	34.7	34.7
DSD	266	321	267	162.3	509	462	502.4	501	253	260	459	509
Depth	296	358	301	191	602	489	627	789	284	290	485	606

primers Elas02_R (5'-CATAGTAGGGTATCTAATCCTAGTTTG-3′) and Tele02_R (5'-GGGTATCTAATCCCAGTTTG-3′; Taberlet et al., 2018). These primer sets target the same region (~163–185 bp), but Elas02 has a higher affinity for elasmobranchs and Tele02 has a higher affinity for bony fishes (Taberlet et al., 2018). Using a combination of 49 different twin-tags (i.e. 2–3 N's and a unique sequence of six nucleotides (De Barba et al., 2014) on both forward and reverse primers), we individually tagged all samples and controls within each PCR run. For details on the PCR setup of eDNA samples, see Text A in Appendix S1.

2.3 | Library building and sequencing

The 12 pools of DNA amplicons were sent to Novogene who performed library building using the TruSeq DNA PCR-free LT Sample Prep Kit (Illumina), with an input of ~750 ng of purified product from each pool. Libraries were then sequenced on an Illumina NovaSeq 6000 using 150 PE sequencing and requesting 10 Gb of output per library.

2.4 | Extraction, amplification and sequencing of fish tissue for reference database

We performed DNA extractions from tissue samples of 87 species of fish (92 specimens), 42 of which at the time did not have complete sequences in GenBank for the 12S rRNA region targeted by the Elas02 and Tele02 primer sets. All of these species are either known to occur in Greenland (Møller et al., 2010) or have been caught in Greenland waters in recent years (GINR, unpublished data). All tissue samples were obtained from the Natural History Museum of Denmark (NHMD), Copenhagen, and most were originally collected from the *R/V Pâmiut* during the GINR's annual bottom trawl survey. Most of the tissue samples are associated with vouchered specimens kept at NHMD (see Table S1 for details). DNA extractions were carried out using the E.Z.N.A.® Tissue DNA Kit (Omega Bio-tek, Cat. no. D3396-01) according to the manufacturer's protocol.

We set up duplicate PCR reactions for each of the 92 specimens using untagged forward primer MiFish-U-F (5'-GTC GGTAAAACTCGTGCCAGC-3′) and untagged reverse primer MiFish-U-R (5′-CATAGTGGGGTATCTAATCCCAGTTTG-3′; Miya

et al., 2015). This primer set was chosen as it amplifies the complete region of the Elas02 primer set (same binding sites), which the primer set Tele02 does not, thus ensuring full reference sequence query coverage for any sequences stemming from the Elas02 primers from the eDNA data. For details on the PCR setup of vouchered tissue samples, see Text B in Appendix S1.

All PCR products showing bands on the gel were then diluted 1:2 with ddH_2O and sent to be purified and commercially Sanger-sequenced (Sanger et al., 1977; Sanger & Coulson, 1975) in both forward and reverse direction by Macrogen Europe. Resulting sequence chromatographs (two forward directions and two reverse directions per specimen) were de novo assembled and manually inspected for errors using Geneious (v.10.0.9; Kearse et al., 2012). For colloquial names and the taxonomy of fishes mentioned throughout the manuscript, we refer to FishBase (https://www.fishbase.org; Froese & Pauly, 2022).

2.5 | Metabarcoding data filtering and analysis

Raw sequencing data were processed using the MetaBarFlow pipeline (Sigsgaard et al., 2022), which primarily involves cutadapt (v3.5; Martin, 2011) with the parameters "--discard-untrimmed --minimum-length 100 -e 0" for demultiplexing, trimming read pairs individually using sickle (v1.33; Joshi & Fass, 2011) with the parameters "sickle se -l 50 -q 28 -x -t sanger -f," and DADA2 (v1.22.0; Callahan et al., 2016) in R (v4.1.2) with the "fastqPairedFilter" function with parameters "minLen = 50, maxN = 0, maxEE = 2, truncQ = 2, matchIDs = TRUE," followed by DADA2 error modelling and error filtering. The most up-to-date version of MetaBarFlow can be found at https://github.com/evaegelyng/MetaBarFlow. We treated the two primer sets as distinct PCR replicates (i.e. as eight PCR replicates per library, four from Elas02 and four from Tele02), although they were run in combined PCR reactions, in order to merge the data stemming from each primer set from the same sample. We specified a minimum read length of 100 bp for both read pairs for a read to be processed. Uniquely identified amplicon sequence variants (ASVs) were then searched against a local version of the GenBank nucleotide (nt) database (downloaded September 27, 2022), specifying a maximum of 500 hits, 90% query coverage and 80% sequence similarity. ASVs were subsequently searched against an additional local database representing the newly generated reference sequences (Table S1) and GenBank sequences from species known to occur in Greenland waters. In cases of ambiguous best hits, taxonomy was assigned as the last common ancestor of the equally well-matching best hits. Hits to species not present in or adjacent to Greenland waters were disregarded in the taxonomic identification. For extended details on taxonomic identification, see Text C in Appendix S1.

We filtered out ASVs with a query coverage <100 or similarities below 98% and filtered out taxa that occurred in higher read counts in the control samples (field blanks, bucket blanks, extraction blanks and PCR blanks) compared with seawater samples, while requiring that taxa were present in at least two out of four PCR replicates (practically in eight PCR replicates, as each PCR reaction consisted of products from both Tele02 and Elas primers). We note that products identified as the same species from Tele02 and Elas primers within the same reaction are not necessarily independent. This is because a template being amplified with the slightly longer Elas primer could subsequently act as a template for amplification with the Tele02 primer and thus generate nonindependent products from the same template. ASVs were collapsed according to their taxonomic identification, after which we performed species rarefaction curves on individual PCR reactions per sample to inspect sequencing depth. We then performed species accumulation curves per sample to inspect species saturation. Samples were then rarefied to the median read number across all sample replicates using the R-package *ROBITools* (v.0.1), after which individual PCR replicates per sample were aggregated and rarefied to the median read number across all samples.

We removed hits to bleak (*Alburnus alburnus*), European perch (*Perca fluviatilis*) and Cyprinidae, which are all freshwater species, as well as hits to Scombridae. The sequences that matched Scombridae had the highest similarity to mackerel tuna (*Euthynnus affinis*), a species, which we have previously worked within our laboratories. We also removed hits to the bird genus *Poecile* and Muscovy duck (*Cairina moschata*), as these, to our knowledge, do not occur in Greenland. The sequences matching these six taxa did not constitute a large contribution to the data (approximately 0.02% of the raw data). We also removed a low abundance sequence matching Atlantic halibut (*Hippoglossus hippoglossus*) from a single sample, as it did not always pass the rarefaction step across different iterations due to its low abundance. Finally, data from the two replicate samples taken per site per depth were collapsed using mean values.

2.6 | Statistical analyses

We used the nonparametric Kruskal–Wallis test (Kruskal & Wallis, 1952) to inspect the influence of sampling area (South, Southeast and Northeast) on taxon richness, as data were not normally distributed. Using area (South, Southeast and Northeast) and depth (Surface or Deep) as predictors, samples were also evaluated for differences in community composition (read count data) using permutational multivariate analysis of variance (PERMANOVA) with 999 permutations and by specifying Bray–Curtis as the distance metric (Bray & Curtis, 1957), using the function *adonis* from the R-package *vegan* (v.2.5.6; Oksanen et al., 2019). Multivariate homogeneity of dispersion was evaluated using the function *betadisper*, and no assumptions were violated. Samples were mapped using the R-packages *rnaturalearth* (v.0.1.0), *rnaturalearthdata* (v.0.1.0), *sf* (v.1.0–1), *sp* (v.1.4–4), *stars* (v.0.5–3) and *tidyverse* (v.1.3.0). Input for nonmetric multidimensional scaling (NMDS) plots was calculated using the functions *vegdist* and *metaMDS* from *vegan* with the Bray–Curtis dissimilarity index and plotted using the R-package *ggplot2*

(v3.2.1; Wickham, 2016). The heatmap was created using the R-packages *pheatmap* (v.1.0.12) and *RColorBrewer* (v.1.1–2).

3 | RESULTS

3.1 | Fish 12S reference sequences from tissue samples

We generated 12S-mtDNA sequences (166–185 bp) using Sanger sequencing for a total of 87 fish species (Table S1), where 42 represent new species additions to the GenBank nucleotide (nt) database for the 12S region covered by the Tele02/Elas02 primers. This leaves ~37 Greenlandic fish species for which barcodes are still lacking (Table S2) and brings the percentage of known Greenlandic fish species with available barcodes for this locus in the GenBank nt database from 74% to 87%. Barcodes and information on vouchered specimens have been deposited in the NCBI GenBank (accession numbers OP863121–OP863212).

3.2 | Seawater eDNA metabarcoding output

We generated a total of 439.40 M read pairs, with an average of 36.62 M read pairs per library (minimum 32.71 M reads, maximum 44.70 M reads, $n = 12$). Across the two primer sets used, we retained 43,999–1,324,017 reads per sample (average of 376,287 ± 25,640 (SEM) reads, $n = 114$) after initial DADA2 filtering. Field blanks ($n = 4$) and bucket blanks ($n = 2$) produced 304–16,242 reads (average of 5968 ± 3662 (SEM) reads) and 67,721–645,622 reads (average of 356,672 ± 166,826 (SEM) reads), respectively. Extraction blanks ($n = 13$) produced 2–339,424 reads (average of 64,050 ± 26,638 (SEM) reads), whereas the PCR blanks ($n = 12$) produced 0–5427 reads (average of 823 ± 558 (SEM) reads). In total, we found 6813 ASVs after chimera removal for the combined set of Tele02 and Elas primers.

3.3 | Contaminants and control samples

A large fraction (~85%) of the data turned out to be human DNA, likely reflecting the bucket sampling method used here. This was particularly evident as field blanks yielded much fewer sequences than bucket blanks did. Importantly, we did not detect any marine fish or mammals in any of our controls including bucket blanks, as nearly all sequences represented human DNA.

After all filtration steps (primarily removal of human sequences), a total of 4.7 M reads remained in our samples. Median read count per sample replicate was 1453 reads, and after aggregating rarefied replicates, each sample contained 11,624 reads. As a result of the relatively low amount of reads passing the filters, all analyses were carried out with data from the two replicate samples per site per depth being pooled with equal weighing.

3.4 | Biological patterns of diversity and distributions in the eDNA data

As a result of the extensive filtering and influence of human DNA, several of the samples did not yield enough sequencing reads to cover the biological diversity within the sample. However, collapsing data from the two samples per site per depth at least partly alleviated this issue. For species rarefaction curves per PCR replicate and species accumulation curves per sample see Figures S2 and S3.

We detected a total of 85 taxa (Table 2). These included 57 fish species (conservatively counting genus level hits once), representing 46 genera and 28 families. We also detected 14 species of marine mammals, two species of terrestrial mammals and 11 bird taxa (Table 2). The detected taxa showed distribution patterns that matched known distributions. For example, Arctic cod (*Arctogadus glacialis*) was only found in the northeast samples, whereas redfish were only found in the south and southeast (Table 2). Among the marine mammals, species with known southern distribution patterns, which comprise all three delphinid species (long-finned pilot whale (*Globicephala melas*), white-beaked dolphin (*Lagenorhynchus albirostris*) and killer whale (*Orcinus orca*)), were only found in the south and southeast samples, whereas the narwhal (*Monodon monoceros*) was primarily found in the northeast samples (Table 2).

We also found some interesting tendencies in the taxa that could not be identified at the species level. For example, the snailfish *Liparis tunicatus/fabricii* was found exclusively in the surface water in the south and southeast samples (up until station 16), whereas it was found almost exclusively in the deeper samples from station 16 and onwards (Table 2). Similarly, the eelpout detections, although not as widely detected, also revealed taxa only present in the south and southeast (greater eelpout (*Lycodes esmarkii*) and *Lycodes gracilis*), as well as taxa only present in the northeast (Canadian eelpout (*Lycodes polaris*), Paamiut eelpout (*Lycodes paamiuti*) and *Lycodes seminudus/reticulatus*). The eelpout taxa were also exclusively detected in deep samples except for a single surface detection of Canadian eelpout at station 22 (Table 2).

Relative read counts indicated a dominance by capelin in the south and southeast samples, whereas northeast samples were dominated by polar cod (*Boreogadus saida*; Figure 2). Redfish and sculpins from *Myoxocephalus* were also relatively abundant, although redfish were primarily found in the deep samples of the south and southeast. Bearded seal (*Erignathus barbatus*) and hooded seal (*Cystophora cristata*) showed contrasting patterns, where bearded seal was almost exclusively detected in surface water samples, whereas hooded seal was found primarily in the deeper samples (Table 2).

Hierarchical clustering of co-occurring taxa (Figure 3) revealed redfish, cod and capelin as the first group of taxa to split, representing fishes primarily from southern areas, whereas Polar cod, ringed seal (*Pusa hispida*), harp seal (*Phoca groenlandica*), Arctic staghorn sculpin (*Gymnocanthus tricuspis*), bearded seal and sculpins from the genus *Myoxocephalus* were the next group to split, largely reflecting a broad detection across the entire latitudinal gradient. The third group to split represented Arctic char (*Salvelinus alpinus*), the

TABLE 2 Systematic presence/absence overview of all fish, marine mammal and bird taxa detected in the eDNA samples in both surface and mesopelagic samples (x), only surface samples (s) or only mesopelagic samples (m). Note that only surface samples were obtained at station 4, and that only detections surviving the rarefaction filter are listed here. Taxonomy follows FishBase, birdsoftheworld.org, and Ugarte et al. (2020). Asterisks indicate taxa that are strictly terrestrial.

	Station																												
	South										Southeast							Northeast											
Taxonomy (family, species)	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Fishes																													
Somniosidae																													
Somniosus microcephalus																s	m												
Lamnidae																													
Lamna nasus			s																										
Rajidae																													
Amblyraja hyperborea																												m	
Amblyraja jenseni																												m	
Clupeidae																													
Clupea harengus	s							s		s							s					s				s		
Argentinidae																													
Argentina silus											m																		
Osmeridae																													
Mallotus villosus	m	x	x	s	x	x	x	x	x	x	x	x	x	s	x	x	m	s	s	s	s	m				x	s		
Salmonidae																													
Oncorhynchus										s							s						m						
Salmo salar					s	s					s								s	m									
Salvelinus alpinus	s		s	s	x	m	x	s	m	m							x	m		s					m	m		x	m
Paralepididae																													
Magnisudis atlantica	m																												
Myctophidae																													
Myctophum punctatum				s																									
Notoscopelus kroyeri	m			s		m				x	m																		
Protomyctophum arcticum					m																								
Bythitidae																													
Bythites fuscus							m																						
Macrouridae																													
Macrourus berglax													m																

(Continues)

TABLE 2 (Continued)

	Station																												
	South										Southeast							Northeast												
Taxonomy (family, species)	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Gaidropsaridae																													
Enchelyopus cimbrius														m															
Gaidropsarus ensis/ argentatus		m		s		s	m	s				x																	
Gadidae																													
Arctogadus glacialis																		m	m	m		x	x	m	m		x	m	m
Boreogadus saida						s		x	s	s		s	s	x	s	x	m	x	x	x	x	x	x	x	x	x	m	x	x
Gadus	x	x	x	s	s	m		s	x	x	m	m			x	m	s				s								
Lotidae																													
Brosme brosme							m				m																		
Gasterosteidae																													
Gasterosteus aculeatus												s		s	s														
Sebastidae																													
Sebastes	m		m	s	x	m	m	m	x	x	m	m	s	m	m	m	s												
Cottidae																													
Artediellus		m						m										m		m									
Gymnocanthus tricuspis					s		s	s	s	s		s		s				s	x	x	s		s		s	s	s	s	s
Icelus spatula/bicornis		m								s			s																
Myoxocephalus	s	x	s		x	x	s	s	x	x		s	s	s	s	s		x	s	s	m	s	x	s	s	s	s	s	s
Triglops murrayi		m	m																										
Triglops pingelii										s			s																
Triglops pingelii/nybelini																	m	s								x	m		m
Agonidae																													
Leptagonus decagonus													s						m										
Psychrolutidae																													
Cottunculus microps												m				m	m			m									
Cyclopteridae																													
Cyclopterus lumpus		s	x	s			s	s	x				s	s		s													
Eumicrotremus spinosus/ derjugini								s																				s	

TABLE 2 (Continued)

	Station																												
	South										Southeast							Northeast												
Taxonomy (family, species)	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Liparidae																													
Careproctus reinhardti																				m									
Liparis bathyarcticus								s					s		s			s	s							s	s		
Liparis tunicatus/fabricii						s	s	s	s	s		s	s	s		m	m	m	m	x		m			m	m	m	m	m
Zoarcidae																													
Gymnelus retrodorsalis/ andersoni		m	s						m																				
Gymnelus viridis															m			m											
Lycenchelys kolthoffi																	m												
Lycodes esmarkii												m																	
Lycodes eudipleurostictus							m	m		m		m		m		m	m		m	m							m	m	
Lycodes gracilis			m				m							m															
Lycodes pallidus								m																				m	
Lycodes polaris																		m	m	m		s			m		m	m	m
Lycodes paamiuti																		m			m	m					m	m	
Lycodes seminudus/ reticulatus																			m			m					m	m	
Stichaeidae																													
Stichaeus punctatus								s	s	s																			
Lumpenidae																													
Anisarchus medius										s			s																
Leptoclinus maculatus		m	m														s			m		s							
Lumpenus lampretaeformis		m										s			s														
Pholidae																													
Pholis gunnellus/fasciata		m			s					s																			
Anarhichadidae																													
Anarhichas		x	m			m	m		s		m		s		m														
Ammodytidae																													
Ammodytes dubius		s				m																							
Ammodytes marinus								s										s						s	s			s	s

(Continues)

TABLE 2 (Continued)

	Station																												
	South										Southeast							Northeast												
Taxonomy (family, species)	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Pleuronectidae																													
Hippoglossoides platessoides		m			s											s													
Reinhardtius hippoglossoides					m		m							m					m										
Mammals																													
Ursidae																													
Ursus maritimus								s									s												
Phocidae																													
Cystophora cristata			m			m	m		m	m		m	m		m	x													
Erignathus barbatus					s	s	x	s	s			s	s	s							s	s		s	s				s
Phoca groenlandica		x					x	m	x	s			s	x		x	m	x	x	m	s				s	m	s	m	
Pusa hispida												s	s	m	s	x		s	m	s		s	x	x	s			x	x
Balaenopteridae																													
Balaenoptera acutorostrata			m								m		s		s														
Balaenoptera physalus			s						s		x	x	x		m	x											s		
Megaptera novaeangliae			s							m			s	x			m												
Physeteridae																													
Physeter catodon		s											s		s														
Monodontidae																													
Monodon monoceros																m		m	m	m	m	s		m	m				
Delphinidae																													
Globicephala melas	m			s							x																		
Lagenorhynchus albirostris											s			s	s														
Orcinus orca			m				s					s					m												
Phocoenidae																													
Phocoena phocoena		x																											
Bovidae																													
*Ovibos moschatus**				s																									
Cervidae																													

TABLE 2 (Continued)

	Station																												
	South										Southeast							Northeast												
Taxonomy (family, species)	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
*Rangifer tarandus**	m	m	s			m	s																						
Birds																													
Anatidae																													
Branta canadensis										s																		s	
Somateria							s											s		s				s					
Columbidae																													
*Columba**					s																								
Alcidae																													
Alle alle																	s												
Cepphus grylle																s													
Fratercula arctica				s																									
Laridae																													
Larus					s				s															s					
Rissa tridactyla																s			s										
Procellariidae																													
Fulmarus glacialis				s												s													
Muscicapidae																													
*Oenanthe oenanthe**													s																
Calcariidae																													
*Plectrophenax nivalis**					s																								

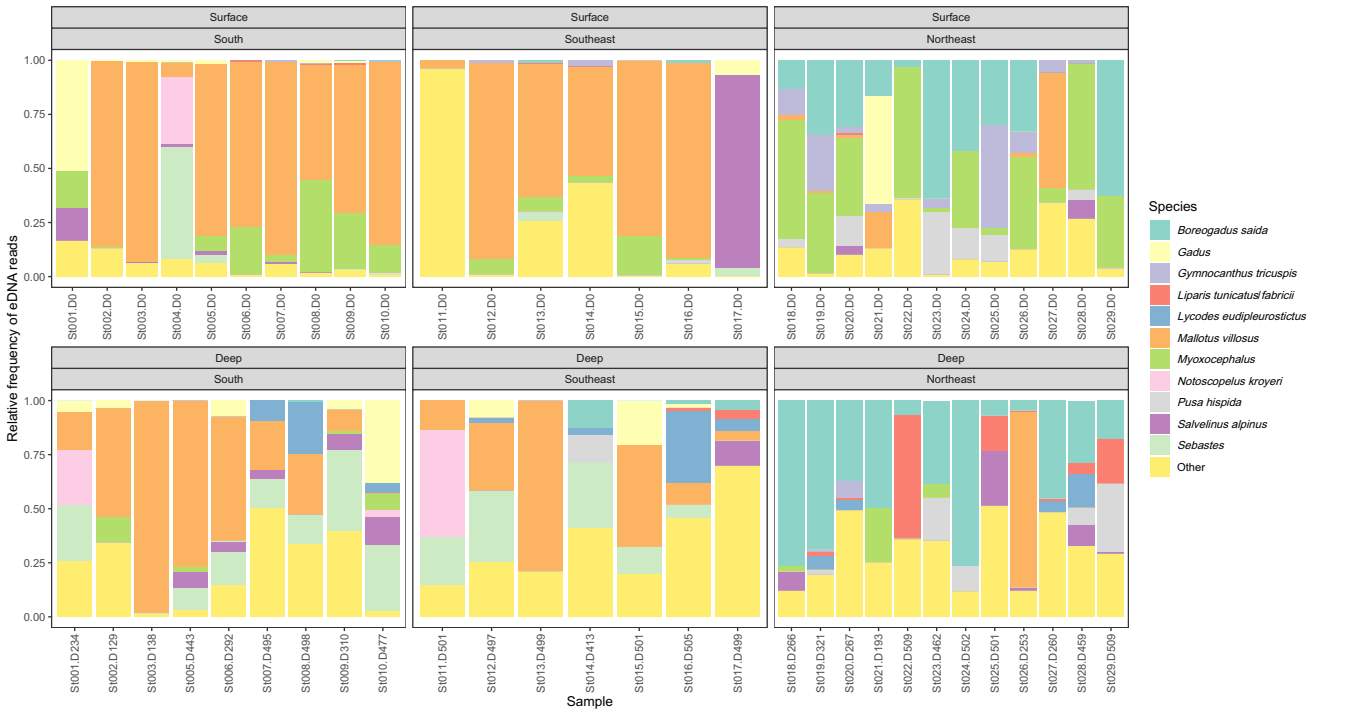

FIGURE 2 Stacked barplot of relative eDNA read frequencies of the 11 most abundant taxa for both deep and surface samples across the South – Southeast – Northeast Greenland gradient. All remaining species are grouped as "other." The two samples taken from each depth at each site are here merged into one with equal relative weighing. The prefix "St" denotes station number, and the suffix "D" denotes the depth (m) at which the samples were obtained.

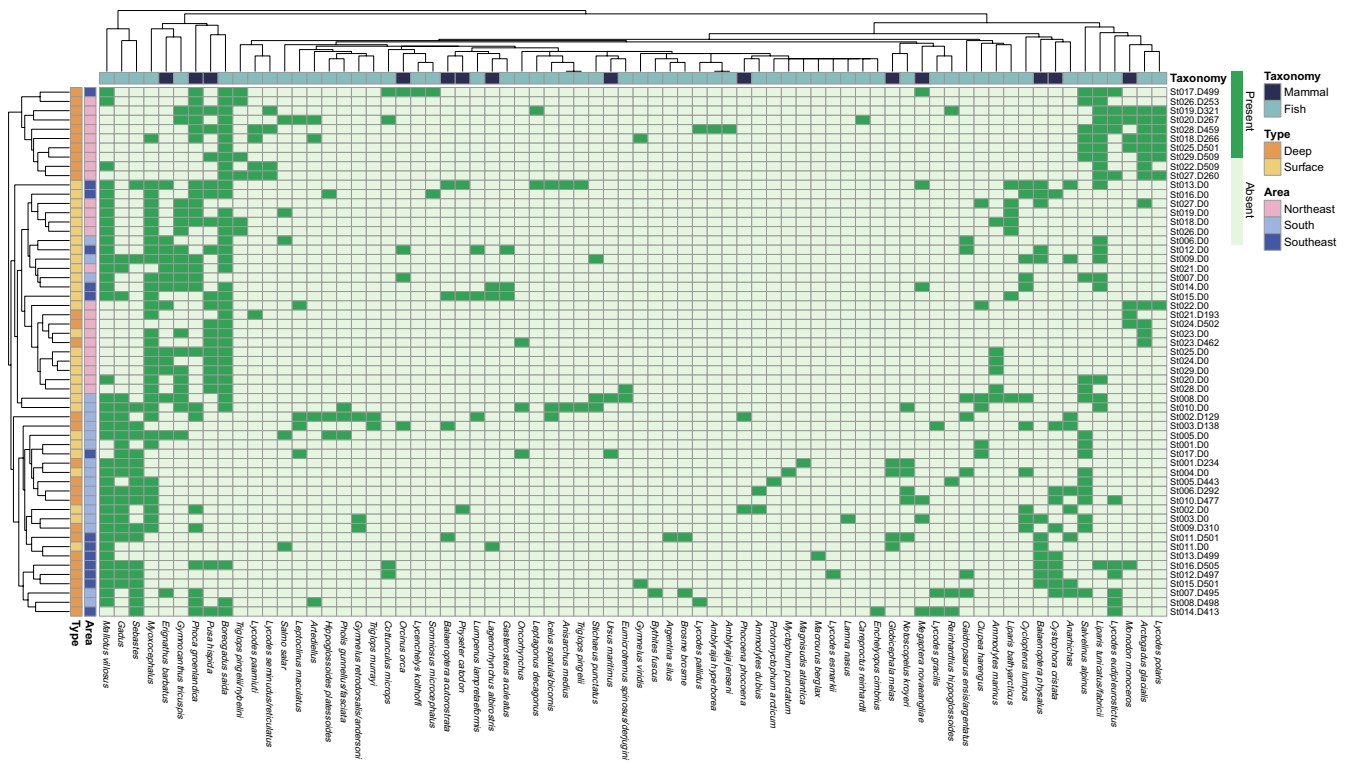

FIGURE 3 Clustered heatmap of fish and marine mammal presence/absence data (dark green vs. light green). The two samples taken from each depth at each site are here merged, and any taxon present in either of the samples is included here. Note that only taxa surviving the rarefaction step are included. Rows are colour-coded according to the type of sample ("Deep" or "Surface") and area ("South," "Southeast" and "Northeast," see Figure 1). Columns are colour coded according to taxonomy ("Fish" or "Mammal"). Row clustering indicates samples with similar community composition, whereas column clustering indicates taxa that frequently occur in the same samples. The prefix "St" denotes station number, and the suffix "D" denotes the depth (m) at which the samples were obtained.

snailfish taxon *Liparis tunicatus/fabricii*, narwhals, Arctic cod and Canadian eelpout, which were mainly detected alongside each other in the northeastern samples, although Arctic char was detected sporadically throughout. Likewise, samples with similar species detections were also largely grouped according to geographic sampling area and the sampling depth (Figure 3), although samples with low amounts of species detected may have blurred this clustering slightly.

Nonmetric multidimensional scaling (NMDS) of the combined samples separated the species communities between the south-southeast and northeast samples for both abundance and presence/absence data (Figure 4a,b). Samples were also grouped according to where in the water column they were obtained (surface or deep, see also Figure S4). The PERMANOVA test showed that 27% of the variation in community composition could be explained by the area sampled (South, Southeast or Northeast, $p < .001$), and 7% could be explained by the depth (Surface or Deep, $p < .001$), whereas the interaction between the two was not significant.

We found a significant difference in taxon richness between the three areas for the surface samples (Kruskal–Wallis test, $p < .05$) but not for the deep samples (Kruskal–Wallis test, $p > .05$), but note that this should be regarded with caution due to the human contamination. The northeast samples generally exhibited a lower taxon richness compared with south and southeast samples (Figure 4c), although with seven species that were specific to the northeast samples (Figure 4d).

We also detected eDNA from several terrestrial mammal species (e.g. musk ox (*Ovibos moschatus*) and reindeer (*Rangifer tarandus*)) and seabirds like little auk (*Alle alle*), black guillemot (*Cephus grylle*), Atlantic puffin (*Fratercula arctica*) and northern fulmar (*Fulmarus glacialis*). While these were not the primary target of this study, they have been included in the list of detected taxa (Table 2).

4 | DISCUSSION

Environmental DNA research has gained increased attention for understanding species distributions in both space and time (Taberlet et al., 2018; Thomsen & Willerslev, 2015). We here demonstrate distribution patterns obtained from eDNA that reflect known species distributions of Arctic fishes and marine mammals. The distributional patterns further indicate a latitudinal shift in species compositions from South to Northeast Greenland both qualitatively and quantitatively. It is inherent to all eDNA studies

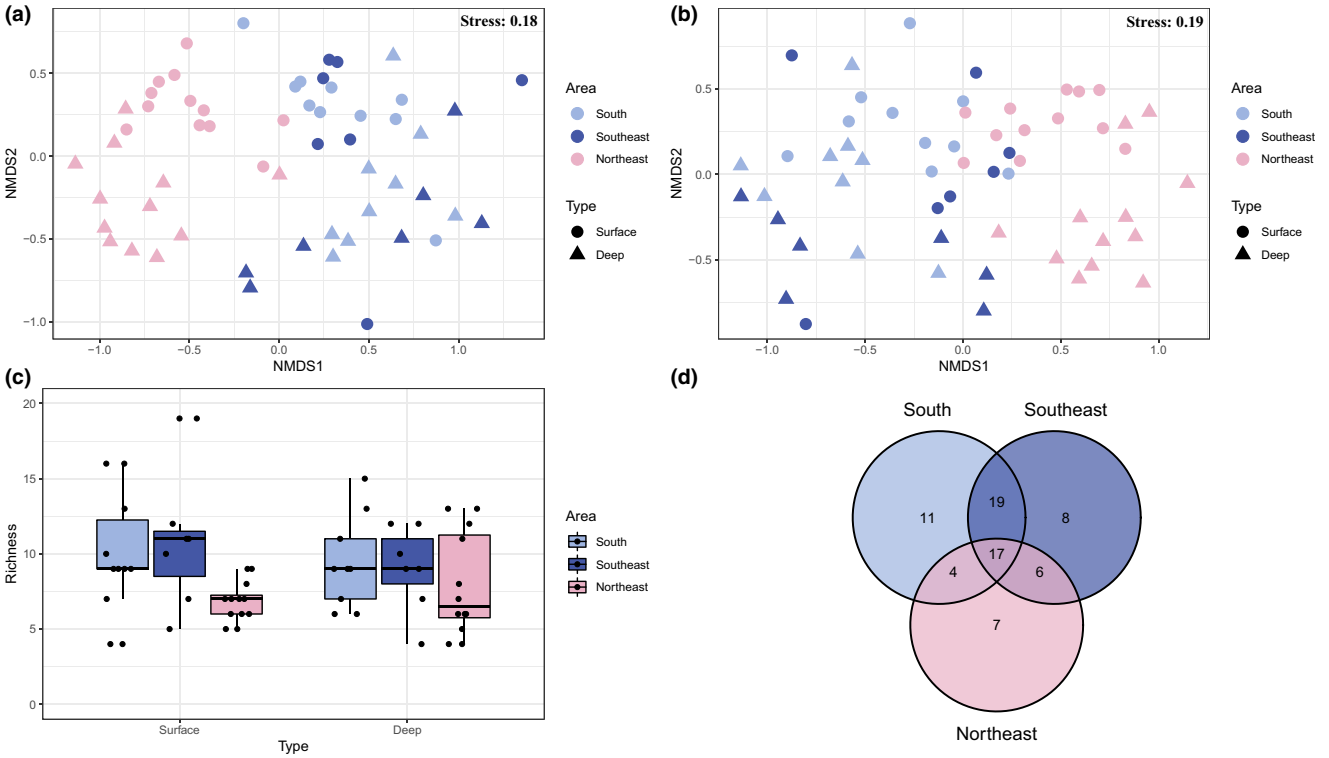

FIGURE 4 Sample ordinations, richness and overlap between marine vertebrates (fishes and marine mammals) detected in South, Southeast and Northeast Greenland. Note that only taxa surviving the rarefaction step are included. (a) Nonmetric multidimensional scaling (NMDS) plot of distances between samples for abundance data using Bray–Curtis as the dissimilarity index. (b) Nonmetric multidimensional scaling (NMDS) plot of distances between samples for presence/absence data using Bray–Curtis as the dissimilarity index. (c) Boxplot of species richness using data from the two combined samples per site per depth. (d) Venn diagram of overlapping species between the three regions. Colours indicate the geographic region where samples were taken, with "South" (light blue) representing stations 1–10, "Southeast" (dark blue) representing stations 11–17 and "Northeast" (pink) representing stations 18–29.

that the absence of species could be due to stochasticity in sampling, PCRs and sequencing. However, given the pervasive human DNA input in this study, we caution to a greater extent than usual, that the absence of species should not be directly interpreted as a species being absent from that location. Specifically for this study, we used less strict filtering than we have done in previous metabarcoding studies (Jensen et al., 2022; Jensen, Sigsgaard, Agersnap, et al., 2021), given the pervasive contamination of human DNA. However, we would argue that the authenticity of the remaining data in this case illustrates that taxa found with two nonindependent primers in one out of four PCR reactions can still be used for establishing species diversity profiles.

4.1 | Biological patterns and known species distributions

The diversity of Greenlandic fishes is well known (Møller et al., 2010), although new species are occasionally described (e.g. Chernova & Møller, 2021; Poulsen, 2015). Additionally, rarely encountered species are still being added to the list, some of which have been ascribed to warming oceans enabling temperate species to move northwards (Møller et al., 2010). We detected eDNA from at least 57 Greenlandic fish species and 14 Greenlandic marine mammal species using opportunistic sampling at two depths per site, despite not sampling in West Greenland, the Greenlandic region with the highest fish diversity (Møller et al., 2010). Based on the recorded specimens from the TUNU expeditions (Christiansen et al., 2021), only 55 fish species have been documented in Northeast Greenland. Furthermore, many of the species listed in Møller et al. (2010) were noted as "rare" or "very rare," and several species would only be expected below the 500 m depths sampled here.

Jørgensen et al. (2015) described a compositional difference between Southeast and Northeast Greenland benthic fish communities based on bottom trawling. We found several examples of fish species detected entirely in the south-southeast (e.g. all three lanternfishes (spotted lanternfish (*Myctophum punctatum*), lancet fish (*Notoscopelus kroyeri*) and Arctic telescope (*Protomyctophum arcticum*)), redfish and wolffish (*Anarhichas*)) or entirely in the northeast (e.g. Arctic cod, sea tadpole (*Careproctus reinhardti*), Canadian eelpout, Paamiut eelpout and *Lycodes seminudus/reticulatus*; Table 2, Figure 4d). This could perhaps indicate preferred thermal ranges or habitat preferences.

The distribution patterns of the detected marine mammal species were consistent with recent literature (Hamilton et al., 2021; Ugarte et al., 2020). The three delphinid species were found primarily in the southern parts, whereas narwhals were primarily found in their hotspot areas in the northeast (Hamilton et al., 2021). Among the marine mammals, the hooded seal was primarily detected in deep waters where they are known to forage, whereas bearded seal was almost exclusively found in surface water samples, which was noted as their preferred habitat by Hamilton et al. (2021).

Levels of eDNA from dominant fish families have shown a good concordance with biomass estimates obtained from bottom trawling (Thomsen et al., 2016). This positive correlation has also been found for single species in both natural (e.g. Salter et al., 2019; Shelton, Ramón-Laca, et al., 2022) and experimental settings (e.g. Karlsson et al., 2022). Our findings suggest that eDNA cannot only detect species across a latitudinal gradient, but that read counts might reflect dominant taxa. This is particularly evident with the clear transition from capelin, known as the keystone ecosystem species in subarctic waters, to polar cod as the dominant keystone ecosystem species in the north (Pedro et al., 2020). Ringed seals were found primarily in the northeast and contributed greatly to the read count data in areas where polar cod was dominating, likely reflecting their preferred source of food. Inferences of trophic interactions based on eDNA data have previously been made with whale sharks (*Rhincodon typus*) and mackerel tuna (Sigsgaard, Nielsen, Bach, et al., 2017). As we here have no other data source to validate actual dominant species at the sampled sites and can only rely on known species distribution patterns, this remains speculative and thus warrants further investigation. However, meticulous quantification techniques from metabarcoding data are on the horizon, and we expect such inferences to become more reliable going forward (Shelton, Gold, et al., 2022).

Sampling eDNA at different depths is known to provide different community inferences (Jeunen et al., 2020; Sigsgaard et al., 2020). All sampling was performed opportunistically and not deeper than ~500 m, which may explain why we failed to detect several explicitly benthic species at the deep stations. This includes species such as Arctic skate (*Amblyraja hyperborea*) and Greenland halibut, which would be expected to occur in large numbers in these areas at greater depths. Although both species were indeed detected, their contribution was minor.

4.2 | Poleward expansions with climate change?

The Arctic is subject to rapid changes as temperatures increase faster in comparison with temperate and tropical areas (AMAP, 2021). Although there are currently somewhat limited fishing activities in the northeast region (Kroodsma et al., 2018), this distinct fish community may be forced poleward because of warmer waters and thus become threatened as fishing activities expand with the retreat of sea ice (Christiansen et al., 2014). With temperatures potentially becoming more favourable for fishes adapted to subarctic environments, interspecific competition from other species may also drive this distinct community further north. Christiansen et al. (2014) stressed the need for understanding impacts on both targeted and bycaught species in light of global change and argued that a precautionary approach is needed as anthropogenic activities expand in the Arctic. If these communities respond to rising temperatures, precise monitoring and modelling tools are needed to elucidate when and how this progress is taking place (Wisz et al., 2015). Christiansen et al. (2016) showed that Atlantic cod, beaked redfish (*Sebastes mentella*) and capelin distributions should already be expected further north than what had previously been reported and argued that input from the warmer Barents Sea may have been a factor in explaining

the newly established species in Northeast Greenland. Andrews et al. (2019) used genetic methods to confirm the boreal input to the Northeast Greenland fish fauna as coming from the Barents sea, by genotyping specimens of Atlantic cod, beaked redfish and northern shrimp and assigning them to ancestral populations. They further argued that given the juvenile stages of the fishes caught, the most likely explanation for the dispersal route was the dispersal of pelagic offspring via advection across the Fram Strait from the Barents Sea to Northeast Greenland. Similarly, Post et al. (2021) found that especially during warmer periods, boreal fish species increased in abundance around the shelf regions of East Greenland in both shallow and deeper waters, and that their lag in response to warming waters could even be used to predict abundances of boreal species in East Greenland. We detected both capelin and cod (*Gadus*) in the northeastern samples but not redfish. Given the sequence overlap in the database for Atlantic cod and Greenland cod (*Gadus macrocephalus*), we cannot discriminate between the two, but we suspect these sequences to represent Atlantic cod as Greenland cod mainly occurs in West and Southwest Greenland (Møller et al., 2010).

Porbeagle (*Lamna nasus*) is a species that in recent years has been reported multiple times from inshore waters of both East and West Greenland (GINR, unpublished data), and our single detection in the south may be an example of ongoing northward expansion potentially related to warming temperatures. We also detected Atlantic herring (*Clupea harengus*) sporadically up to 73°N, which is further north than the northernmost (70°N) documentation in East Greenland that we are aware of (Nielsen, 1953). Atlantic salmon (*Salmo salar*) was detected sporadically up to 73°N, and local citizens in Ittoqqortoormiit have also reported catches of Atlantic salmon in recent years. However, as both species are regularly consumed and occasionally also found as laboratory contaminants, we regard these findings with caution. The sporadic detections of the salmonid genus *Oncorhynchus* likely represent signals from the recently discovered invasion of pink salmon (*Oncorhynchus gorbuscha*) in Greenland waters (Nielsen et al., 2020), although the sequences had slightly better matches with chum salmon (*Oncorhynchus keta*).

Presence of eDNA from the lesser sandeel (*Ammodytes marinus*) at 73°N fuels the debate on whether this species inhabits East Greenland waters—an uncertainty arising from large similarities in morphological characters among *Ammodytes* species (Mecklenburg et al., 2018). This species is known from west of Svalbard and around Jan Mayen (Wienerroither et al., 2011) and our finding cannot be regarded as a potential poleward expansion, rather as a confirmation of its presence in Northeast Greenland. We stress that the lesser sandeel has an identical barcode to small sandeel (*Ammodytes tobianus*) and great sandeel (*Hyperoplus lanceolatus*) for this marker, but these two species appear less likely to occur in East Greenland. Nevertheless, detecting several of these fishes at or near their marginal distribution illustrates the accuracy of eDNA samples for pinpointing close to exact distribution patterns. This suggests that eDNA sampling can be helpful in elucidating potential range shifts, even at small spatial scales, in future monitoring of remote, Arctic regions. Sampling along a latitudinal gradient as done here could also help reveal if transitional patterns of dominant species (e.g. capelin vs. polar cod) move further north as climate change progresses. An important caveat to our sampling approach is that the northeast samples were primarily taken at sheltered locations inside the Kaiser Franz Joseph Fjord, whereas the majority of the south- and southeastern samples were obtained from the mouth of the fjords in more open areas. Our sampling design was too minimalistic to ascertain the effects of both habitat types (sheltered or unsheltered) and overall sampling area, which would be important to fully elucidate the latitudinal patterns in species composition along this gradient. To properly demonstrate such transitional patterns, we would encourage a rigorous sampling design taking into account both short-term (Ely et al., 2021; Jensen et al., 2022), seasonal (Sigsgaard, Nielsen, Carl, et al., 2017; Stoeckle et al., 2017) and yearly variation in fish abundances, while also accounting for primer bias, potentially skewing the relative abundance measurements towards specific taxa (Kelly et al., 2019). This could potentially be achieved using automated eDNA samplers (Hansen et al., 2020). Such sampling design should also seek to standardize at which depths and at how many depths in the water column the samples should be taken, as well as take into account the habitat type of the sampling sites, which we were not able to do here.

4.3 | Limitations of DNA target fragments and database coverage

While eDNA metabarcoding has become increasingly used for marine biological monitoring, this still entails many pitfalls. The mitochondrial 12S region used here has been proposed as a better-targeted marker for fishes compared with the mitochondrial cytochrome oxidase 1 (COI; Collins et al., 2019). However, we urge the continuous sequencing and reporting of complete mitochondrial genomes as a priority in the coming years, for enabling better in-depth analyses of species-level and population-level analyses. For example, our setup was unable to resolve the taxon *Liparis tunicatus/fabricii* to species level here, as the barcodes for these two species were identical for the marker used. The sequences representing these two species were detected only in surface waters up until station 14 and then almost exclusively in the deep samples from station 16 onwards (Table 2). This may reflect the two preferred species habitats, with kelp snailfish (*Liparis tunicatus*) representing the shallow detections and gelatinous snailfish (*Liparis fabricii*) representing the detections in the deep samples. The same could be true for the taxon *Triglops pingelli/nybelini*, where some sequences were possible to assign to ribbed sculpin (*Triglops pingelli*) and others matched equally well to both species. We suspect that the *Triglops pingelli/nybelini* taxon likely represents bigeye sculpin (*Triglops nybelini*), given the predominant detection in deep samples.

Obtaining barcodes from multiple individuals of each species is critical for establishing ranges of both inter- and intra-specific variation, as it enables us to search for barcode gaps between species. While we assigned ASVs matching *Amblyraja* to species level, we caution that

e.g. shorttail skate (*Amblyraja jenseni*) was assigned based on a single sequence that we ourselves generated in this study (100% match) and with only a single basepair difference compared with Arctic skate. Shorttail skate is listed as rare (Møller et al., 2010) and was detected further north than we would have expected. This could be because of overlapping barcodes with other skate species (e.g. Arctic skate or starry ray (*Amblyraja radiata*)) where only few individuals have been sequenced. Furthermore, the validity of shorttail skate as a separate species from Arctic skate has been questioned previously (Coulson et al., 2011; Naylor et al., 2012), although they appear divergent with regards to tooth row meristics (Mecklenburg et al., 2018).

In future eDNA studies, new primer sets developed from complete mtDNA references for all species of interest could allow better discriminatory power coupled with higher specificity for the targeted species. It might also be possible to extend this framework to new barcode regions with the potential for population-level inferences of single species (e.g. Baker et al., 2018; Dugal et al., 2022; Parsons et al., 2018; Sigsgaard, Nielsen, Bach, et al., 2017) or multiple species either through metabarcoding or target capture approaches (e.g. Jensen, Sigsgaard, Liu, et al., 2021; Turon et al., 2020). Such population-level inferences could help elucidate or confirm the suspected migratory routes used for boreal fish input to the northeast waters of Greenland, by determining dominant haplotypes and their ancestry across sampling sites in Greenland, as has been done using tissue samples previously (e.g. Jacobsen et al., 2021).

4.4 | Implications in light of global change

We here show that near-exact geographical and bathymetric distribution patterns of both fishes and marine mammals can be obtained using eDNA samples. We argue that this approach is highly relevant in remote settings such as the east coast of Greenland, where logistic constraints make regular biomonitoring difficult. Despite the high proportion of human DNA in our samples, we were still able to extract meaningful biological information from just 15% of the data, and minor adjustments in the sampling protocol could easily eliminate this issue.

Greenland is expected to be further impacted by climate change in the future, primarily through a reduction in sea ice extent, increasing temperatures and ocean freshening (Sejr et al., 2017; Wassmann et al., 2011). This may enable boreal input to establish amidst the Arctic fauna in the northeast areas. Proper monitoring tools that can effectively document such changes are a necessity. Given the precision of eDNA metabarcoding in detecting marginal distribution ranges, we advocate for frequent and continuous implementation of eDNA approaches in surveys that monitor how biological communities respond to climate change, for example by documenting species range expansions in remote areas such as Northeast Greenland.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The raw sequencing data and usage notes are available on Dryad. The data can be accessed at https://doi.org/10.5061/dryad.pnvx0k6qv. Any enquiries should be directed to the corresponding author.

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BIOSKETCH

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Author contributions: MRJ, PFT and SR conceived the ideas for the project. MRJ, SH and SR conducted the eDNA sampling in Greenland. PRM, SWK and JN contributed tissue samples for the reference barcodes. MRJ analysed the data and drafted the manuscript with input from all authors. All authors approved the final version.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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