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ORIGINAL ARTICLE

Arctic nekton uncovered by eDNA metabarcoding: Diversity, potential range expansions, and pelagic-benthic coupling

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Abstract

The Arctic Ocean is home to a unique fauna that is disproportionately affected by global warming but that remains under-studied. Due to their high mobility and responsiveness to global warming, cephalopods and fishes are good indicators of the reshuffling of Arctic communities. Here, we established a nekton biodiversity baseline for the Fram Strait, the only deep connection between the North Atlantic and Arctic Ocean. Using universal primers for fishes (12S) and cephalopods (18S), we amplified environmental DNA (eDNA) from seawater (50–2700 m) and deep-sea sediment samples collected at the LTER HAUSGARTEN observatory. We detected 12 cephalopod and 31 fish taxa in the seawater and seven cephalopod and 28 fish taxa in the sediment, including the elusive Greenland shark (*Somniosus microcephalus*). Our data suggest three fish (*Mallotus villosus*, *Thunnus* sp., and *Micromesistius poutassou*) and one squid (*Histioteuthis* sp.) range expansions. The detection of eDNA of pelagic origin in the sediment also suggests that *M. villosus*, *Arctozenus risso*, and *M. poutassou* as well as gonatid squids are potential contributors to the carbon flux. Continuous nekton monitoring is needed to understand the ecosystem impacts of rapid warming in the Arctic and eDNA proves to be a suitable tool for this endeavor.

KEYWORDS
biodiversity, carbon flux, cephalopods, deep sea, fish, Fram Strait

1 | INTRODUCTION

The Arctic Ocean hosts a large biomass of uniquely adapted organisms. Its diversity is poorly sampled but intermediate relative to the world's oceans (~8000 extant species; Bluhm et al., 2011; Hardy et al., 2011). New Arctic animal taxa are still frequently discovered and described (Archambault et al., 2010; Darnis et al., 2012; Walczyńska et al., 2018); however, the Arctic diversity is also at risk. Between 1970 and 2011, the abundance of Arctic freshwater and marine populations has declined by 81% and 36%, respectively (Senapati et al., 2019). The Arctic Ocean faces the world's fastest warming (Gille, 2002; Walczowski & Piechura, 2006),

which has notably resulted in a reduction in sea-ice coverage and an alteration of circulation patterns (Fossheim et al., 2015) such as "atlantification."

"Atlantification" refers to the process whereby North Atlantic water is flowing increasingly further northward, ultimately resulting in Arctic water temperatures that are more similar to the North Atlantic Ocean (Polyakov et al., 2017). Atlantification may lead to the northward retreat of large, long-lived, and slow-growing Arctic organisms and their replacement by comparatively smaller, short-lived, and fast-growing boreal species (Walczyńska et al., 2018). This "borealization" (Kraft et al., 2013) of the Arctic has already been documented in crustaceans (see references in Polyakov et al., 2020 e.g., Dalpadado et al., 2012; Eriksen et al., 2017; Orlova et al., 2010, 2015) and fishes (Fossheim et al., 2015; Haug et al., 2017). Nektonic species such as cephalopods and fish may be particularly good indicators of borealization, because they may actively adjust their depth and geographic distribution to find optimal environmental conditions over relatively short time scales.

The Arctic is inhabited by 32 cephalopod species (15 families; Xavier et al., 2018). Most of these cephalopods occur occasionally in the Arctic as low temperatures and salinity prevent year-round presence (Golikov et al., 2017). Ten species complete their entire life cycle in high Arctic latitudes, including octopuses, sepiolids, and pelagic squid (Xavier et al., 2018 and references therein). A total of 242 fish species (45 families) are documented in the Arctic and adjacent waters. Most of these species (53%) belong to the suborders Cottoidei (72 species) and Zoarcoidei (55 species; Mecklenburg et al., 2010). Of these 242 species, 100 are exclusively Arctic species while 142 are arctic-boreal, predominantly boreal, or boreal species (Mecklenburg et al., 2010).

Distributions of Arctic fishes are impacted by increasing temperatures, prey availability, and declining sea ice. Several boreal fish species have been expanding northward in the last decade (Fossheim et al., 2015; Haug et al., 2017), while the distribution area and biomass of polar resident fish were reduced (Eriksen et al., 2017; Hop & Gjøsæter, 2013). Range expansions of Atlantic species into the Arctic ecosystem may lead to changes in trophic interactions (Johannesen et al., 2012), for example, as a result of increased predation pressure and intensified competition (Fossheim et al., 2015; Kortsch et al., 2015; Wiedmann et al., 2014). The distribution of some cephalopods has also changed with climate change. *Gonatus fabricii* is now found in Arctic regions, which were previously too cold for this species (Golikov et al., 2012, 2013). Simultaneously, warm-water cephalopods have also been reported in the Arctic (Golikov et al., 2014). Biodiversity and distribution data of Arctic marine fishes and cephalopods are (1) incomplete in many areas due to insufficient sampling and (2) changing as a result of climate change. Altogether, this calls for efficient efforts to monitor Arctic nekton in hotspots of change.

The Fram Strait, the only deep connection between the North Atlantic Ocean and Arctic Ocean, has become a model region to study Arctic climate change and faunal range expansions. It is a transition zone of warm Atlantic water flowing poleward as the West Spitsbergen current (WSC), and of Arctic Waters flowing southward as the East Greenland Current (EGC; Figure 1a; Gascard et al., 1995; Walczowski et al., 2005). Ice coverage in the Fram Strait has decreased in the last decades (Hansen et al., 2013). To monitor the Fram Straits' upper water column and benthic ecosystems, the Alfred Wegener Institute, Helmholtz-Centre for Polar and Marine Research (AWI), established the LTER HAUSGARTEN, which is situated west of Svalbard (Soltwedel et al., 2005). Since 1999, annual cruises sample 21 stations at the LTER HAUSGARTEN. These efforts have resulted in a unique time series on mega-, macro-, meiobenthic, and prokaryotic fauna, as well as biogeochemical and geological processes (Bauerfeind et al., 2009; Bergmann et al., 2009; Hoste et al., 2007; Nöthig et al., 2015). Regional studies have mostly focused on the benthic fauna and mesozooplankton (Christiansen et al., 2016), and knowledge on nekton diversity and distribution in the Fram Strait remains limited.

The expansion of nekton species into new areas may result in changing food web dynamics and in altered carbon fluxes. Most research focusing on carbon flux in the Fram Strait concentrates on vertical particle export (e.g., Forest et al., 2010; Møller et al., 2006; Pedersen et al., 2005; Sherr et al., 2003). Continuous observations in the Fram Strait show that climate change is slowing down the biological carbon pump due to sea-ice-derived meltwater stratification (von Appen et al., 2021). Sinking phytoplankton, ice-algae, and fecal pellets are the two major sources of sinking organic carbon in the Fram Strait (Bauerfeind et al., 1994, 2005; Birgel et al., 2004; Lalande et al., 2016; Wassmann et al., 1996). Yet, oxygen consumption rates of arctic deep-sea benthos suggest that the organic matter supply, as measured by common sediment traps, has been underestimated by at least one order of magnitude (Christensen, 2000). One source of pelagic carbon that is still poorly quantified are sinking carcasses of medium-sized fishes and cephalopods (1–100 cm). The detection of these food falls is difficult due to temporal and spatial variability of deposition, high scavenging rates, and logistical challenges to observe them in situ (Stockton & Delaca, 1982). In the Fram Strait, the only reported food falls are a decapod carcass in the Molloy Deep at 5551 m depth (Klages et al., 2001) and a fish carcass at 1280 m depth west off Svalbard (Soltwedel et al., 2003). To evaluate the importance of nekton food falls in the Fram Strait biological carbon pump, insight in the kinds of organic matter that reach the seafloor is required.

Environmental DNA (eDNA) metabarcoding has proven to be a powerful tool for biodiversity assessment and species detection and offers major advantages over conventional monitoring methods (Boussarie et al., 2018; Creer et al., 2016). It is particularly suitable for the study of nekton, which is known to avoid nets (Collins & Rodhouse, 2006; Wormuth & Roper, 1983; Xavier et al., 2016). Metazoan diversity of the Arctic coastal and slope ecosystems has been studied with eDNA analysis (Grey et al., 2018; Lacoursière-Roussel et al., 2018; Leduc et al., 2019; Sevellec et al., 2021; Thomsen et al., 2016), but similar studies that target open ocean nekton are lacking. The only cephalopod eDNA studies focusing on general distributions and community compositions were conducted in the North Atlantic (Merten et al., 2021; Visser et al., 2021). Here, we analyzed cephalopod and fish eDNA in Arctic seawater and sediments from the LTER HAUSGARTEN observatory to (i) establish a

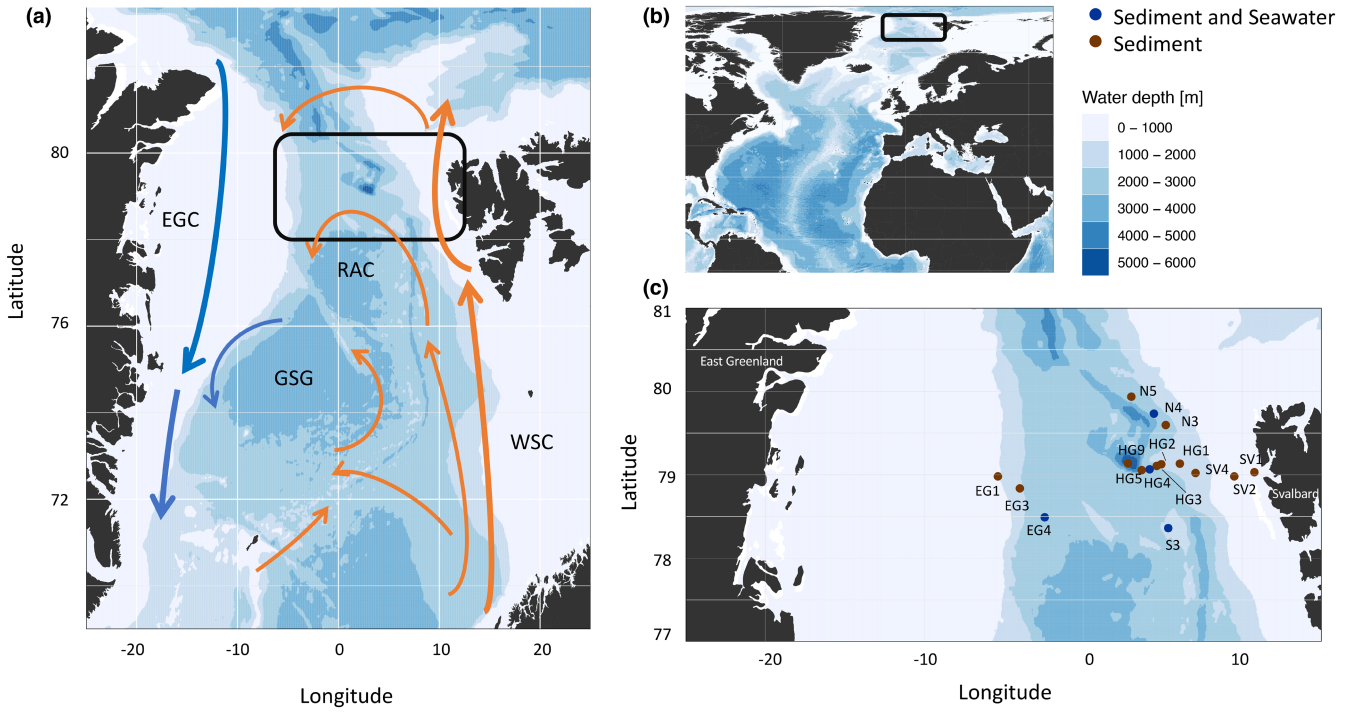

FIGURE 1 Arctic Ocean off Greenland and Svalbard. (a) Current system of the North Atlantic Ocean and Arctic Ocean. WSC, West Spitzbergen Current; RAC, Return Atlantic Current; EGC, East Greenland Current; GSG, Greenland Sea Gyre. The orange arrows indicate warm, Atlantic water, and the blue arrows cold, Arctic water. The black square shows the sampling area. (b) The study site at the Fram Strait of the Arctic Ocean is depicted by the black box. (c) Sampling sites for collecting sediment (brown dots) or seawater and sediment (blue dots) for eDNA metabarcoding of cephalopods and fishes in the Fram Strait.

nekton biodiversity baseline, (ii) detect range shifts linked to global warming ("atlantification"), and (iii) identify taxa that may contribute to the local carbon flux.

2 | MATERIALS AND METHODS

2.1 | Sample collection, filtration, and DNA extraction

Seawater samples for eDNA metabarcoding were collected during the cruises PS121 in August/September 2019, MSM95 in October/November 2020, and PS126 in May/June 2021 in the Fram Strait (Figure 1c). Samples were taken in triplicate between 50 m and above the bottom (between 2250 and 2705 m deep) at three stations (S3, HG4, and N4) in 2020 and four stations (S3, HG4, N4, and EG4) in 2019 and 2021, resulting in a total of 282 samples (Figure 2).

Sampling was conducted using 12-L Niskin bottles mounted on a CTD rosette. During the cruises PS121 and PS126, 6 L were filled from one Niskin bottle into either three 2 L bottles or one 10 L bottle that were previously cleaned with bleach and flushed with MilliQ water. On cruise MSM95, we had the opportunity to directly filter the water from the Niskin bottles by attaching the tubing needed for filtration. In each case, 2 L of water were filtered with a peristaltic pump using 0.22 µm Sterivex-GP filters (Merck Millipore). For filtration controls, MilliQ water was filtered instead of seawater at every station. The Sterivex filters were sealed with caps and stored at −80°C until further processing in the laboratory. DNA was extracted from the filters using the DNeasy Blood and Tissue Kit (Qiagen) with a modified protocol (Methods S1). DNA extracts were stored at −20°C until further processing.

Sediment samples were collected with a multicorer during the cruises PS121 and PS126 at 16 stations (Figure 1c). Sediment samples were taken from three cores from the multicorer by scooping the first 3 cm during PS121 and 1 cm during PS126 of surface sediment into sterile Falcon tubes. The sediment samples were stored at −20°C until further processing. DNA from the sediment was extracted using a DNeasy Power Soil Kit (Qiagen) in combination with a QIAvac 24 Plus Vaccum Manifold and the updated DNeasy Power Soil Pro Kit (Qiagen) in combination with a Tissue Lyser II, following the manufacturer's protocol. Sediment DNA was eluted in 2 × 30 µL Solution C6 (10 mM Tris) and stored at −20°C.

For both seawater and sediment extractions, a DNA extraction control was included consisting of MilliQ instead of samples and PCR-negative controls to check for potential contamination in the laboratory. Rigorous precautions were taken to reduce contamination (see Methods S1).

2.2 | Library preparation and sequencing

The seawater and sediment eDNA was amplified with two universal primer sets, one targeting the nuclear 18S rRNA gene of cephalopods (Ceph18S_forward 5′-CGCGGCGCTACATATTAGAC

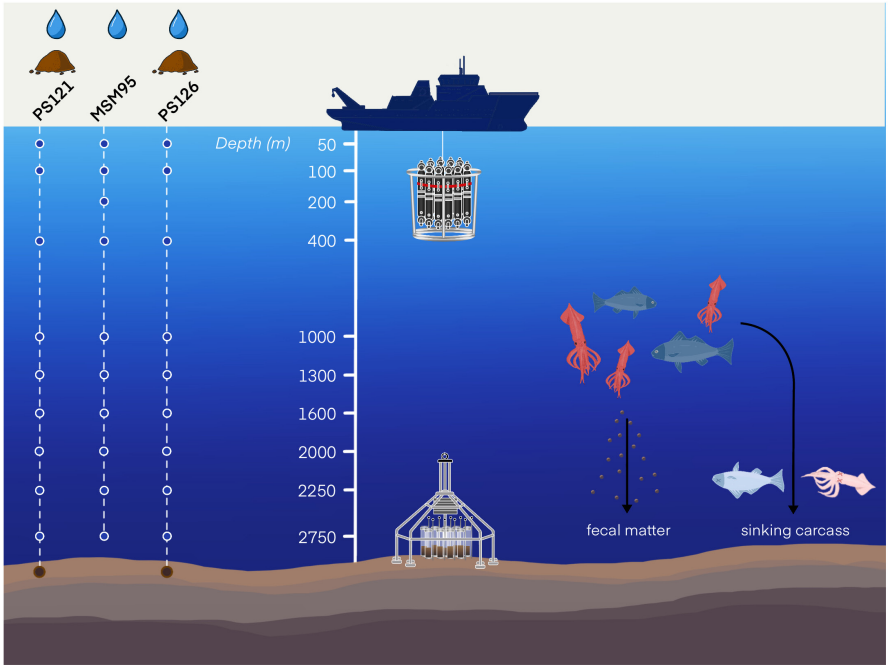

FIGURE 2 Sampling scheme during the cruises PS121, MSM95, and PS126. Seawater was sampled with a CTD rosette at nine depths during PS121 and PS126, and at 10 depths during MSM95. Sediment was sampled with a multicorer. Seawater and sediment were analyzed for diversity of fish and cephalopod eDNA.

and Ceph18S_reverse, 5′-GCACTTAACCGACCGTCGAC; amplicon length 140–190 bp; de Jonge et al., 2021) and the other one targeting the mitochondrial 12S rRNA gene of fishes (teleo_F: 5'-ACACC GCCCGTCACTCT and teleo_R: 5'-CTTCCGGTACACTTACCATG; amplicon length 80–100 bp; Valentini et al., 2016). All samples were amplified in PCR triplicates via a 1-Step PCR (Table S1), resulting in nine PCR products per sampling depth and site. Positive (DNA extract of two fish or cephalopod species that do not occur in the Arctic or Atlantic Ocean and a mock control including 50% of each species) and negative PCR controls (PCR-grade water instead of DNA extract) were added to every PCR plate (Methods S1). After PCR, all samples were pooled with equimolar concentrations resulting in a total of five libraries that were sequenced in five sequencing runs (Table 1). The sequencing runs targeting cephalopods were processed on an Illumina MiSeq with the MiSeq Reagent Kit v3, 600 cycles (PE), 2×300 bp (Illumina), and the sequencing runs targeting fish were processed on an Illumina MiSeq with the MiSeq Reagent Kit v2, 300 cycles (PE), 2×150 bp (Illumina). The sequencing runs targeting fish eDNA in sediment were processed in collaboration with the Alfred Wegener Institute (AWI) in Bremerhaven, Germany, and the remaining sequencing runs were conducted at the Institute of Clinical Molecular Biology (IKMB) in Kiel, Germany.

2.3 | Bioinformatic analysis

After sequencing, the obtained reads were demultiplexed by the sequencing center. The PCR primers were removed using cutadapt (version 1.18; Martin, 2011). Only sequences including both the forward and reverse primer were used for further analysis using the Diverse Amplicon Denoising Algorithm (see Method S1, DADA2, version 1.16.0, Callahan et al., 2016).

2.4 | Taxonomic assignment of reads

For cephalopods, the taxonomic assignment of the samples and all controls were performed as in Merten et al. (2021). Briefly, cephalopod sequences from the SILVA 18S database were searched against the NCBI GenBank database (accessed in June 2020) until no further cephalopod sequences were found, resulting in 169 sequences from 119 species. The reference database for cephalopods was then assembled by combining these cephalopod sequences with all other eukaryotic 18S rRNA sequences from the SILVA database to prevent spurious assignments of non-cephalopod amplicons.

For fishes, the MIDORI 2 database of 12S gene sequences based on NCBI GenBank release 248 was used (Leray et al., 2022). The files provided were reformatted to be usable with the IDTAXA program (Murali et al., 2018).

Nonmarine species were excluded from the complete dataset. For negative, filtration, or extraction controls, we subtracted the maximum number of reads found for that amplicon sequence variant (ASV) from the corresponding ASV in all samples connected to that respective control. Remaining sequences with less than 10 reads were discarded. We refrained from changing taxonomic assignments from genus level to species level in cases where a genus only included one known species from the Fram Strait. As the species diversity is under-sampled in the Arctic, we do not know whether those assignments might belong to cryptic species or unknown species and we therefore decided to apply a conservative approach to prevent misinterpretation.

2.5 | Statistical analysis

All statistical analyses were conducted in RStudio version 3.6.3 (R Core Team, 2021; RStudio Team, 2020). We refrained from

TABLE 1 Summary of the sequencing runs for cephalopods (Ceph18S) and fish (teleo) and corresponding total number of reads (# reads) after sequencing and DADA2 analysis as well as the mean and standard deviation of reads per sample.

Sequencing run	# reads after sequencing (mean ± SD)	# reads after DADA2 (mean ± sd)	# ASVs after cleaning	# taxa
Ceph18S MSM95, sw	6,090,710 (56,395 ± 147,115)	5,407,110 (50,066 ± 130,431)	23	6
Ceph18S PS126, sw & sed	3,846,048 (13,542 ± 30,689)	3,147,100 (23,311 ± 137,805)	41	SW: 10 SED: 7 Total: 13
Teleo PS121, MSM95, sw	5,701,698 (20,363 ± 31,573)	5,543,889 (19,800 ± 30,893)	45	24
Teleo PS121, sed	3,746,327 (18,011 ± 55,634)	3,647,036 (17,534 ± 54,540)	22	18
Teleo PS126, sw & sed	6,790,533 (44,383 ± 38,063)	6,485,805 (42,391 ± 36,489)	56	SW: 23 SED: 27 Total: 33

Note: In addition, the number of ASVs after cleaning of the dataset (Tables S2–S4) and number of taxa that could be assigned to the ASVs are given. The number of samples analyzed is given, including eDNA samples, negative controls (negC), and positive controls (posC).
Abbreviations: sed, sediment; sw, seawater.

comparing the taxa composition between the three different years, as the cruises took place in different seasons and are therefore not comparable. As a result, we pooled the taxa detections of all 3 years for further analysis. For the seawater fish eDNA data, the different depths were binned into shallow (50–400 m), medium (1000–2000 m), and deep (2250–2705 m) depths in order to test whether the taxa composition changed with depth. All analyses were conducted with presence/absence data and the read count data for comparison. We did not perform corrections on the read count data, as we do not infer abundance or biomass estimates of taxa. A Bray–Curtis (for read count data) or Jaccard (for presence/absence data) index matrix was created, to construct nonmetric multidimensional scaling (NMDS) plots using the package *vegan* with the function "metaMDS" (Oksanen et al., 2019). We then performed a permutational multivariate analysis of variance (PERMANOVA) using distance matrices with the function "adonis" (package *vegan*) to test whether statistically significant differences between the different depth bins existed. When the PERMANOVA was significant, we used the package *pairwise.adonis* (Martinez, 2020) to indicate which depth bin was significantly different. For the comparison between sediment and seawater diversity, we constructed Venn diagrams. Species accumulation curves were created for each sampling type (sediment and seawater) and taxonomic group (cephalopod and fish) using the "specaccum" function in *vegan* to determine the effect of sampling effort on overall taxa richness.

3 | RESULTS

3.1 | Taxa accumulation analysis

While the taxa accumulation curve for cephalopod richness showed an increasing trend, the taxa accumulation plots of seawater and sediment for fish were close to reaching a plateau (see Figure S2). This indicates that the sequencing depth and number of stations sampled were nearly sufficient to depict the total fish diversity in the area, but insufficient to detect total cephalopod diversity.

3.2 | Sequencing results for cephalopods

3.2.1 | Total cephalopod diversity and depth distribution from eDNA samples

After cleaning of the sequencing data (Table 1), a total of 15 cephalopod taxa were detected in seawater and sediment samples taken during two consecutive years (2020, 2021) of which six were identified to species (40%), three to genus (20%), four to family (27%), and two to higher taxonomic levels (13%; Table S2). Four taxa were detected in both seawater and sediment samples (27%), eight taxa occurred only in seawater samples (53%), and three taxa only in sediment samples (20%) (Figure 3a).

Seawater

The most frequently detected cephalopod taxon in seawater was Gonatidae (36%, n = 13), which also had the highest number of reads (85%, n = 234,369; Figure 4a). Gonatidae was followed by Teuthida for most detections (22%, n = 8) and read numbers (10%, n = 28,343). However, the read number was at least eight orders of magnitude higher for Gonatidae than for any of the other detected taxa. In terms of eDNA detections at different depths, Gonatidae and Teuthida were followed by *Gonatus* sp. (11%, n = 4 depths), *Rossia palpebrosa* (8%, n = 3), *Vampyroteuthis infernalis* (6%, n = 2), and *Loligo forbesii* (6%, n = 2). All other taxa were detected at only one depth. The number of reads followed the same trend, except that *V. infernalis* had more reads (2%, n = 4223) than *Gonatus* sp. (1%, n = 2929) and *R. palpebrosa* (0.5%, n = 1450). *Teuthowenia maculata* had 2073 reads (0.8%) and *L. forbesii* 1670 reads (0.6%). All other taxa had read counts below 1000 (<0.5%). Gonatidae and Teuthida were detected across the entire water column, from

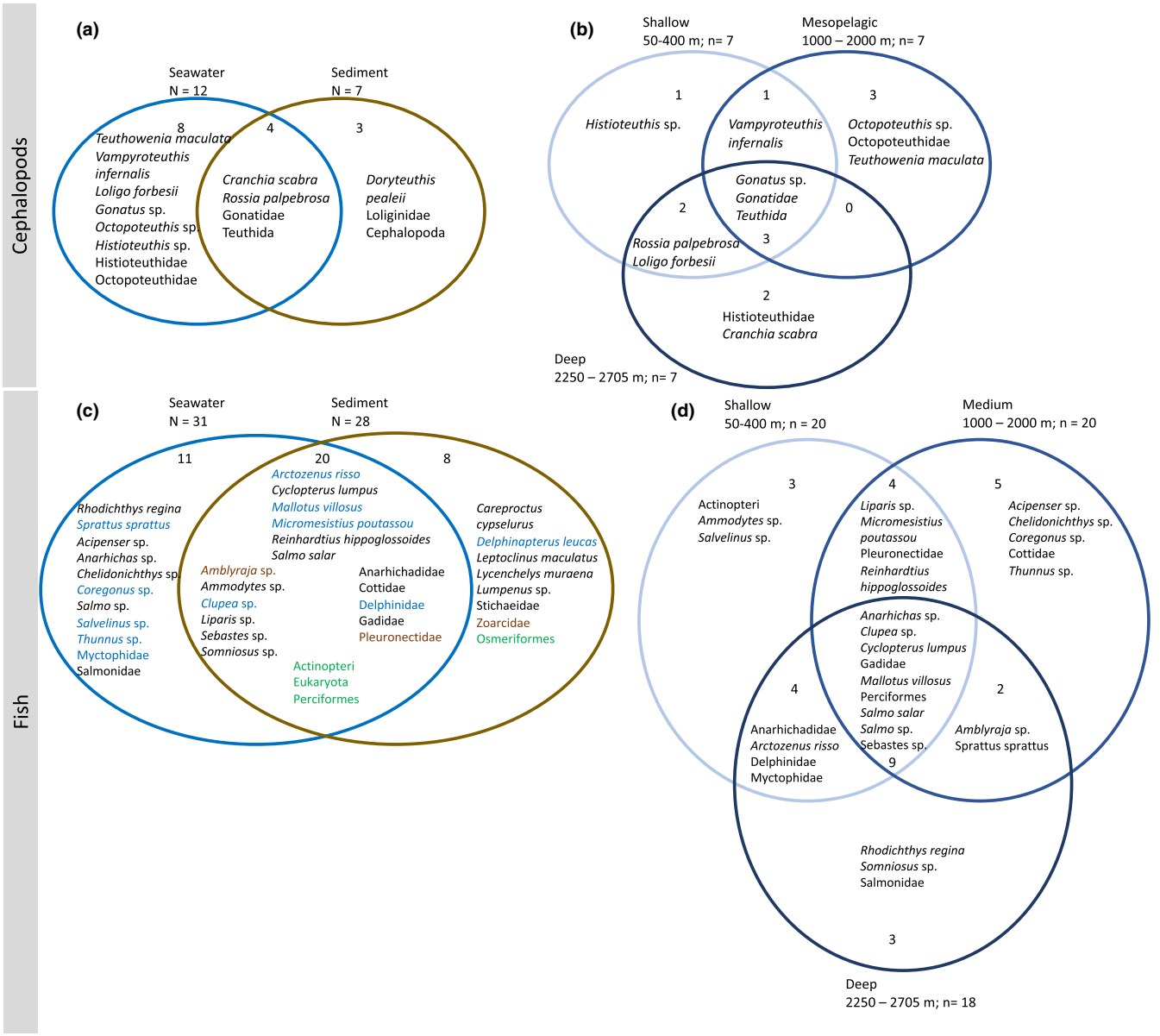

FIGURE 3 Venn diagrams showing cephalopod and fish taxa detected with eDNA metabarcoding from the cruises PS121 in 2019 (only fish), MSM95 in 2020 and PS126 in 2021. (a) Venn Diagram showing the cephalopod taxa richness detected in seawater ($n = 12$) and sediment ($n = 7$) with eDNA metabarcoding in the Fram Strait, Arctic Ocean. The samples were taken during two cruises in 2020 (MSM95) and 2021 (PS126). The taxa detected in both sediment and seawater samples are depicted by the overlapping circles ($n = 4$). (b) The cephalopod taxa are grouped in depth bins. Each circle represents a depth bin: shallow (50–400 m), medium (1000–2000 m), and deep (2250–2705). Overlapping circles show taxa that were detected in more than one depth bin. (C) Comparison between fish taxa found in seawater and sediment eDNA samples. Brown = benthic taxa, blue = pelagic taxa, black = benthopelagic or demersal taxa, green = no assignment to one of the above-mentioned categories. (d) Comparison of fish richness between different depths. The taxa are grouped in depth bins.

shallow to deep depths (see Figure S3). *Gonatus* sp. and *R. palpebrosa* were detected above 200 m and below 1900 m. *Histioteuthis* sp. was present at 50 m depth and Histioteuthidae at 2500 m. While our detections may include *Gonatus steenstrupi* and/or *G. fabricii*, the primers used were not able to identify the corresponding ASVs to species level. To be conservative, we refer to *Gonatus* sp. for eDNA detections assigned to Gonatidae and *Gonatus* sp. in the following discussion.

Sediment

The sediment samples also showed Gonatidae and Teuthida having the highest read counts (34%, $n = 5050$ and 28%, $n = 4190$, respectively) and most detections (31%, $n = 5$ and 19%, $n = 3$, respectively; Figure 4b, Figure S4). *Cranchia scabra* eDNA was detected with high read numbers in the sediment (20%, $n = 3001$) while fewer reads were present in seawater samples ($n = 72$). *Doryteuthis pealeii* was the only species exclusively detected in sediment samples. Overall,

FIGURE 4 Percent of the sequence reads (purple bars) and eDNA detections (green bars) in seawater and sediment of cephalopod eDNA samples taken during two cruises in 2020 (MSM95) and 2021 (PS126). The taxa highlighted in orange are dubious. (a) The 12 cephalopod taxa detected in seawater samples. (b) The seven cephalopod taxa detected in sediment samples.

fewer cephalopod taxa were detected in the sediment compared with seawater (7 vs. 12 taxa).

Dubious taxa

Of the 15 detected cephalopod taxa, eight are only known from regions south of 60°N (*T. maculata*, *V. infernalis*, *L. forbesii*, *Octopoteuthis* sp., Octopoteuthidae, *Cranchia scabra*, *D. pealeii*, and Loliginidae) and hence are dubious detections. All of these taxa were detected in one or two samples, and each contributed less than 1.5% (seawater) and 6% (sediment) of sequencing reads, except of *C. scabra* which had a relatively high read count of 20% in the sediment.

3.3 | Sequencing results for fish

3.3.1 | Total fish diversity and depth distribution from eDNA samples

After cleaning the sequencing data (Table 1) and combining the results from the sediment and seawater stations, we were able to detect 39 taxa (Tables S3–S5). Nine of them were identified to family (23%), 14 to genus (36%), 12 to species level (31%), and four to higher taxonomic levels (10%). Most detected taxa in seawater and sediment were pelagic (28%, $n = 11$), followed by benthic and benthopelagic (both 26%, $n = 10$) taxa. Another 21% ($n = 8$) could not be assigned to one group because they included species or life stages that were either benthic or pelagic. The detected taxa belonged to 21 different families. Twenty taxa were found in both the sediment and the seawater samples (Figure 3c). Ten of these taxa were benthopelagic (*Cyclopterus lumpus*, *Reinhardtius hippoglossoides*, *Salmo salar*, *Ammodytes* sp., *Liparis* sp., *Sebastes* sp., *Somniosus* sp., Anarhichadidae, Cottidae, and Gadidae), five of them were pelagic (*Arctozenus risso*, *Mallotus villosus*, *Micromesistius poutassou*, *Clupea* sp., and the marine mammal taxa Delphinidae), and two were benthic taxa (*Amblyraja* sp. and Pleuronectidae). Three of the taxa shared between sediment and seawater samples were Actinopteri, unidentified Eukaryota, and Perciformes. They cannot be assigned to one of the categories used here. Eleven taxa were detected only in seawater, represented by six benthopelagic (*Rhodichthys regina*, *Anarhichas* sp., *Chelidonichthys* sp., *Acipenser* sp., *Salmo* sp., and Salmonidae) and five pelagic taxa (*Sprattus sprattus*, *Thunnus* sp., *Coregonus* sp., *Salvelinus* sp., and Myctophidae). Eight taxa were detected exclusively in the sediment, five of which were benthopelagic or demersal (*Careproctus cypcelurus*, *Leptoclinus maculatus*, *Lycenchelys muraena*, *Lumpenus* sp., and Stichaeidae), one benthic (Zoarcidae), one purely pelagic (*Delphinapterus leucas*), and one taxon that cannot be assigned to a category (Osmeriformes). We detected eDNA of *Somniosus* sp. once in seawater (2420 m) and once in the sediment (Station HG1, 2508 m bottom depth).

Seawater

In the seawater samples analyzed for fish eDNA, 31 taxa could be assigned of which seven were identified to family (22%), 13 to genus (42%), eight to species (26%), and three to lower levels (10%). For the following analysis, only taxa assigned to class or higher were included (therefore excluding Eukaryota). *Mallotus villosus* was the taxon that was most often detected (in 81% of the sampled depths, $n = 29$, total number of sampled depths = 36) and also had the highest number of reads (44% of the total read count, $n = 186{,}022$; Figure 5a). The second most often-detected taxa were Gadidae (72%, $n = 26$) and Perciformes (53%, $n = 19$), however, with low read counts of only 4.5% ($n = 19{,}132$) and 2% ($n = 9297$), respectively. These two taxa were followed by *Sebastes* sp. (50%, $n = 18$) and *Clupea* sp. (42%, $n = 15$), which also had the second and third most read counts with 11% ($n = 45{,}900$) and 14% ($n = 59{,}447$), respectively. *Cyclopterus lumpus* was detected in 33% of the sampled depths ($n = 12$) and represented in 4% ($n = 16{,}824$) of the reads. *Sprattus sprattus* and *S. salar* followed with 17% ($n = 6$) and 14% ($n = 5$) of detections and were represented in 1.5% ($n = 6414$) and 3% ($n = 12{,}883$) of the read counts, respectively. Pleuronectidae and Myctophidae were detected in 14% ($n = 5$) of depths and less than 0.5% of read counts. *Salmo* sp. and Delphinidae were represented in 11% ($n = 4$) of sampled depths (read count 3% $n = 12{,}883$ and 0.1% $n = 489$, respectively). All other taxa were detected in less than 10% of the sampled depths and in less than 0.5% of read counts.

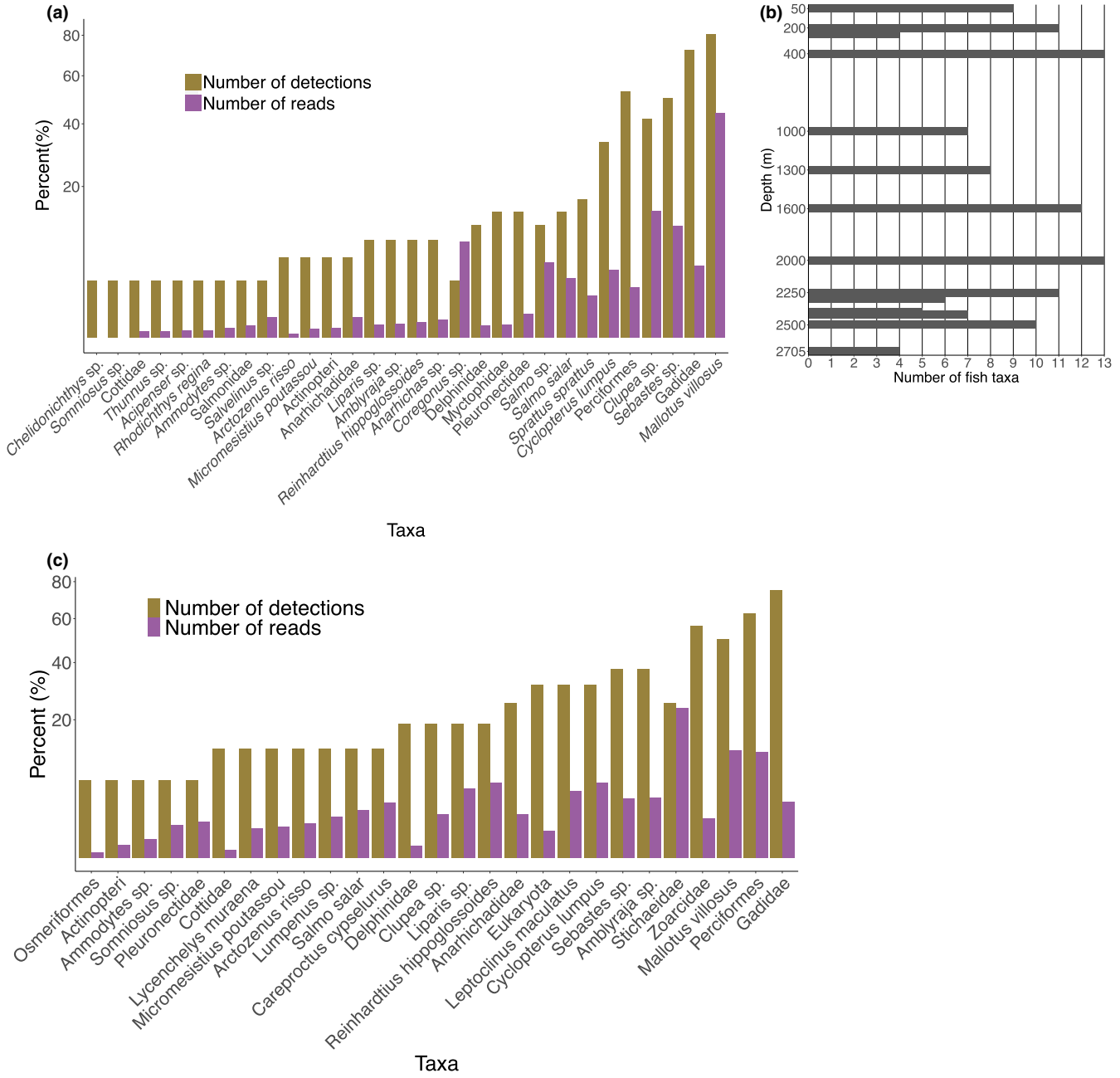

FIGURE 5 Fish taxa detected in seawater of the Fram Strait by eDNA metabarcoding. The taxa detection Eukaryota is excluded. The purple bars represent the frequency of occurrence of sequencing reads and the green bars represent the frequency of occurrence of taxa detections. (a) Percentage of the fish and dolphin taxa detected with eDNA metabarcoding for all three cruises pooled. (b) Number of individual taxa detected with eDNA metabarcoding at depths between 50 and 2705 m at four stations (pooled) in the Fram Strait. (c) Fish taxa detected in sediment of the Fram Strait during the cruises PS121 in 2019 and PS126 in 2021.

Sediment

Twenty-seven fish taxa could be identified in the sediment (Figure 5c) of which seven were assigned to family (25%), seven to genus (25%), 10 to species level (36%), and four to higher taxonomic levels (14%). At all 16 sampled stations, fish eDNA was detected. In contrast to the seawater samples, the sediment samples did not show the same trend between the frequency of occurrence of detections and sequencing reads (Figure 5c). eDNA of Gadidae was detected at 75% of the sampled stations ($n = 12$), but only contributed 3% to the overall sequencing reads ($n = 8437$). The same is true for Zoarcidae which was detected in 56% of stations ($n = 9$), but was represented in only 2% of sequencing reads ($n = 4251$). However, Perciformes and *M. villosus* were among the most often-detected taxa in sediment with 63% ($n = 19$) and 50% ($n = 8$) of detections, respectively, and also were among the highest sequencing read counts with both 12% ($n = 30,203$ and 31,438, respectively). The most abundant taxon in terms of sequencing reads was Stichaeidae with 24% ($n = 61,152$). All other taxa contributed less than 6% to the overall sequencing reads

($n < 15{,}500$). *Amblyraja* sp. and *Sebastes* sp. were all detected in 38% ($n = 6$) of the stations, and all other taxa were detected in less than 32% of stations ($n < 6$).

Dubious taxa

Three detected fish taxa were not known to occur in the Arctic Ocean. *Careproctus cypselurus* (falcate snailfish) was detected in sediment at two stations (HG1 and HG2) in relatively high sequencing read numbers ($n = 8152$). *Sprattus sprattus* (European sprat) was detected in relatively high sequencing read numbers ($n = 6414$) in seawater at depths between 1600 and 2300 m. *Chelidonichthys* sp. (gurnard) was detected in low read numbers ($n = 12$) in seawater at 2000 m at only one station (EG4).

3.4 | Fish species richness in relation to depth

When pooling all stations, the number of fish taxa per depth varied between four and 13 (Figure 5b). Most taxa were detected at 400 m ($n = 13$), 1600 ($n = 12$), and 2000 m ($n = 13$). The bottom depth differed between 2250 and 2705 m at the different stations. However, when comparing the individual stations, the peak number of fish taxa richness was present in deeper depths as well (see Figure S5). The station EG4 was only sampled in 2 years (2019 and 2021) and had the highest number of fish taxa at 400 and 2500 m ($n = 6$). The other stations were sampled in all 3 years and showed peak numbers of taxa at 2000 m (HG4, $n = 12$), 50 m (N4, $n = 9$), and 2250 m (S3, $n = 9$).

The number of taxa per depth range varied between 18 and 20. The species composition between shallow, medium, and deep depths overlapped with nine taxa occurring at all three zones, while three, five, and three taxa only occurred in shallow, medium, or deep depths, respectively (Figure 3d). NMDS plots based on Jaccard (stress = 0.10, eDNA presence/absence) and Bray–Curtis indices (stress = 0.16, sequencing read abundance) both showed a close clustering of fish community composition at shallow (50–400 m) and medium (1000–2000 m) depths, while the community composition of deep depths (2250–2705) clustered distinctly (Figure 6). We found significant differences in fish community composition between the three depth bins based on Jaccard indices (PERMANOVA: $r^2 = 0.30$, $p < 0.005$, Table S6), which was explained by significant differences in shallow and medium depths compared with deep depths (pairwise.adonis: shallow vs deep: $r^2 = 0.27$, $p = 0.018$; medium vs deep: $r^2 = 0.23$, $p = 0.042$). Shallow and medium depth bins showed no significant differences in taxa community composition based on presence/absence data (pairwise.adonis: $r^2 = 0.19$, $p = 0.130$). However, the same comparison between shallow, medium, and deep depths proved not significant based on Bray–Curtis indices (PERMANOVA: $r^2 = 0.15$, $p = 0.362$, Table 2). Differences between the NMDS plots based on the Jaccard and Bray–Curtis indices are expected, as the two only provide the same results when all species are equally abundant, which never happens in natural communities.

4 | DISCUSSION

We present the first survey of nekton diversity in the Fram Strait with an eDNA metabarcoding approach. Seven cephalopod and 39 fish taxa were detected, including the elusive Greenland shark (*Somniosus microcephalus*). The results suggest range expansions of the fish taxa *M. villosus*, *M. poutassou*, and *Thunnus* sp. and of the squid *Histioteuthis* sp. The detection of nekton eDNA in the sediment also suggests that *M. villosus*, *A. risso*, and *M. poutassou* as well as gonatid squids are potential contributors to the regional carbon flux.

4.1 | Diversity and potential range expansions of cephalopods and fishes in the Fram Strait

Environmental DNA from the Fram Strait seawater revealed seven cephalopod taxa that are known from the Arctic or North Atlantic and eight taxa that were dubious detections. The high abundance of the squid *Gonatus* sp. in Arctic waters (Golikov et al., 2017) was reflected in the high eDNA read counts and detections for this taxon in our samples. The detection of Histioteuthidae and *Histioteuthis* sp. in our samples is unexpected as histioteuthids are so far only known from the North Atlantic (Jereb & Roper, 2010). Except for one

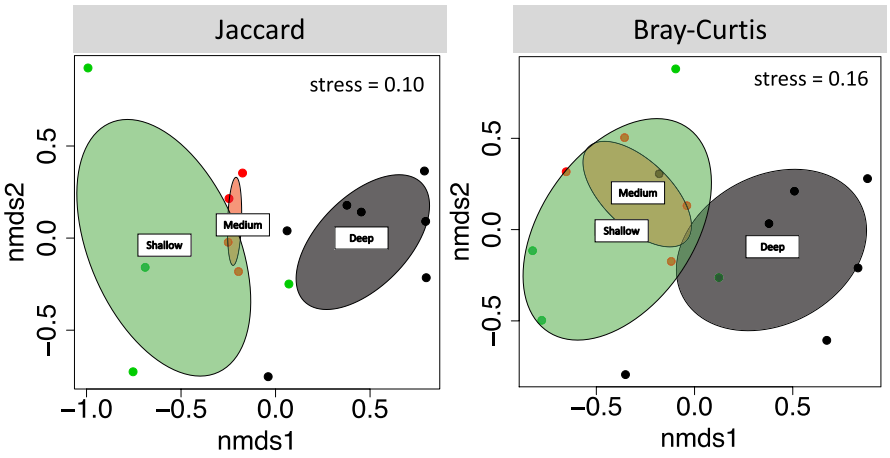

FIGURE 6 NMDS plots based on fish eDNA detections and sequencing read counts from seawater samples collected in the Fram Strait. Left: Differences in taxa richness based on Jaccard indices (eDNA presence/absence data) between shallow (50–400 m), medium (1000–2000 m), and deep (>2000 m) depths are shown. Right: Same comparison between the three different depth bins based on Bray–Curtis indices, taking the sequencing read number into account.

specimen of *Histioteuthis bonnellii*, that was caught in the Davis Strait (West Greenland; Kristensen, 1980). The known distribution of *H. bonnellii* in the North Atlantic equals that of *Teuthowenia megalops* (Jereb & Roper, 2010), a species that has expanded its range to the Arctic likely via warm, northward flowing Atlantic currents (Golikov et al., 2013). The same currents could have transported *Histioteuthis* sp. specimens further north.

Of the 39 unique fish (and dolphin) taxa, capelin (*M. villosus*) was the most often-detected taxon and the taxon that had most read counts per sample. This species inhabits the northern boreal Atlantic at the margins to cold Arctic waters south from the Fram Strait (Rose, 2005). Previous accounts recorded capelin as far north as 76.14°N and 9.03°W, off the Northeast Greenland shelf break (Christiansen et al., 2016). Our data suggest a range expansion of capelin 424 km further north up to 79.7°N and also further to the west to 2.41°W toward the Greenland ice shelf. Throughout history, capelin has shown a strong colonizing ability when large-scale environmental changes occurred. During interglacial periods, it migrated from the North Pacific to the North Atlantic and then further into the Barents Sea toward Iceland and southern West Greenland (Rose, 2005). As capelin responds quickly to environmental change, this key species in the Atlantic and Arctic food web has been referred to as an "early warning sea canary" for ecosystem changes (Jákupsstovu & Reinert, 2002; Rose, 2005).

The presence of *Thunnus* sp. eDNA at 78.6°N suggests another fish range expansion. In 2012, three bluefin tuna were captured more than 1500 km further south than our eDNA detections in the Denmark Strait. This was the first scientifically confirmed presence of this species in east Greenland waters in more than 300 years (MacKenzie et al., 2014). Species distribution models project after 2040 a decrease in the relative abundance of bluefin tuna in most of its current North Atlantic distribution area and an increase toward the north such as around Svalbard (Erauskin-Extramiana et al., 2019). Occasional migrations of tuna further north are likely associated with increased water temperatures and prey species immigration (MacKenzie et al., 2014). Indeed, eDNA of *Thunnus* sp. was detected in the southernmost part of our study area, which was dominated by warmer Atlantic water masses (sea surface temperature at the time of water sampling: 6°C). We also detected tuna prey species including herring (*Clupea* sp.), sand lance (*Ammodytes* sp.), and Gadidae including blue whiting (*M. poutassou)* (Chase, 2002; Logan et al., 2011). A third fish range expansion was blue whiting (*M. poutassou*), which we detected at 79.7°C which is more than 900 km further north than its known distribution. In East Greenland waters, the northernmost distribution of blue whiting is 71.4°N (Post et al., 2019) and fisheries surveys rarely catch this fish (Bergstad et al., 2018). Distributional shifts and range expansions of gadids in the Pacific Arctic have recently been documented (Wildes et al., 2022). We expected to repeatedly detect Greenland halibut (*R. hippoglossoides*) and Arctic skate (*Amblyraja hyperborean*) since they occur in high relative abundance in the Fram Strait, but these taxa were only represented in low read numbers and in relatively few samples.

The potential range expansions and the absence of eDNA of previously abundant species highlights that Arctic communities are changing and suggest ongoing borealization in the Fram Strait. Borealization will have ecosystem implications; the first symptoms of this process have been documented and are in line with our data (Walczyńska et al., 2018). The northward shift of boreal species including cod may have led to intensified competition among the few large predators in the Arctic. The resulting reduction in abundance may explain the low number of detections of large predatory species (e.g., halibut) in our eDNA data. Indeed, fisheries data show a decrease in abundance of Greenland halibut between 2004 and 2012 in the Barents Sea. Changes in prey species, size, or quality may also contribute to the disappearance of nekton species (Walczyńska et al., 2018). For instance, in the northern distribution range of cod, off the coast of Newfoundland and Labrador, capelin has migrated southward due to ocean cooling, resulting in reduced prey availability for cod. This has led to diminishing cod populations as a result of poor body conditions and lower reproductive success (Rose & O'Driscoll, 2002; Vilhjálmsson, 1997). Long-term, but also occasional range expansions of highly mobile predators with high dispersal potential such as tuna, may lead to changes in their abundance and distribution and will impact spawning and migratory behavior, regional food webs, and fisheries (Muhling et al., 2017), also potentially in the Fram Strait.

4.2 | The vertical dimension of nekton eDNA

The fish eDNA richness in the water column had a peak in the upper 400 m and close to the bottom between 1600 and 2500 m. Although we did not sample between 400 and 1000 m water depth, the observed trend seems similar to the Pacific Ocean. Here, pelagic fish diversity (collected with net trawls) peaks at around 200–300 m and then decreases with depth with the lowest species richness and number of species below 2000 m (Smith & Brown, 2002). The peak close to the bottom between 1600 and 2500 m could also stem from accumulated or resuspended eDNA from the sediments. eDNA is more concentrated and decays slower in sediments than in seawater (Sakata et al., 2020; Thomsen & Willerslev, 2015; Turner et al., 2015).

We detected benthic fish taxa in epipelagic samples. These detections may result from eDNA of the larvae of the corresponding taxa. For instance, the family of cod-like fishes Gadidae are typically benthic. However, eDNA has been detected in the water column between 200 and 2705 m. Larvae of Gadidae reside in shallow depths between 10 and 30 m, and adults of some species inhabit the benthopelagic layer down to 600 m, while other species such as the Arctic cod descends down to 1300 m (Froese & Pauly, 2000). Similarly, liparid eDNA was detected between 50 and 1600 m. *Liparis* larvae preferentially stay between 10 and 200 m and as adults descend to deeper layers down to 1700 m (Coad, 2017; Coad & Reist, 2004; Froese & Pauly, 2000). The vertical eDNA distribution of *Gonatus* sp. is in line with its known depth distribution and ontogenetic migration. As juveniles, *Gonatus* sp. reside in epipelagic layers and

as they mature they perform ontogenetic migration to meso- and bathypelagic depths (Kristensen, 1983). The females of *Gonatus* sp. produce a single egg mass which is brooded at bathypelagic depths (Seibel et al., 2005). After a single reproductive event, the females die and presumably sink to the seafloor as is known for gonatids in the Gulf of California (Hoving et al., 2017). This life history strategy suggests annual pulses of gonatid carcasses to the seafloor (Hoving et al., 2017), also in the Fram Strait. We detected *Gonatus* sp. eDNA in Arctic marine sediments which likely stemmed from feces or foodfalls.

We also detected eDNA of the pelagic fish species spotted barracudina, capelin, and blue whiting in the sediment. Capelin is the only species that is associated with the bottom when they spawn between 12 and 300 m deep (Thors, 1981). However, all sediment samples were collected at depths greater than 2000 m. Therefore, the capelin eDNA in sediment could originate from predator defecation (Dawe et al., 1998; Dolgov, 2002; Kristensen, 1984; Taberlet et al., 2018). Another source of eDNA could be the selective or sloppy feeding by squids. Squids have a narrow esophagus and are restricted in the prey tissue they can ingest. *Gonatus* and other squids therefore discard bony parts and heads of their prey which results in a flux of tissue and hence eDNA to the seafloor (Lipinski, 1987; Sakurai et al., 2013, Hoving pers. obs. for *Gonatus*). The fish primer *teleo* unexpectedly resulted in detections of Delphinidae and *D. leucas* (beluga) in particular. The corresponding ASV for Delphinidae assigned to the species *Lagenorhynchus albirostris*, *Peponocephala electra*, and *Feresa attenuate*, but only the white-beaked dolphin *L. albirostris* occurs in the Arctic Ocean (Galatius & Kinze, 2016). The detection of beluga eDNA corresponds with the known distribution of beluga in Arctic and subarctic waters where they dive to depths of 1000 m or more, often to the seafloor (O'Corry-Crowe, 2018). As eDNA of both taxa were detected in sediment, its origin could stem from foodfalls or feces. Based on the wide horizontal distribution and high abundance of these cetaceans in the Arctic food web, they may play an important role in the regional carbon cycle via the consumption of prey, the release of feces, and the deposition of their carcasses on the seafloor.

4.3 | The use of eDNA to monitor nekton diversity in the Fram Strait

We successfully detected a large portion of the known Arctic fish and cephalopod diversity, indicating that eDNA is a suitable tool to monitor nekton diversity in the Fram Strait. eDNA is transported to a certain extent via currents; however, it is simultaneously decayed and diluted quickly beyond PCR detection limits (Murakami et al., 2019; Port et al., 2016; Shea et al., 2022; Thomsen & Willerslev, 2015). Hence, we can expect our eDNA detections to be recent and to originate from the area where it was released. In addition, our results are in line with the literature suggesting that eDNA metabarcoding can be used to elucidate potential range expansions in the Arctic (Jensen et al., 2023). The 12S primer for fish (*teleo*) did not differentiate all taxa to species level. This was particularly problematic for the family Gadidae (e.g., Atlantic and Polar cod) as documented before (Thomsen et al., 2016). The 12S primer was able to detect 93% of the fish families captured by trawling in the subarctic of Greenland (Thomsen et al., 2016), and their total number of detected taxa (37 taxa) was similar to our results (35 taxa, excluding dolphin and dubious taxa), highlighting the general efficiency of the primer. However, in our data, 32% of the fish eDNA detections were identified to species level, while this was much more in Thomsen et al. (2016; 65%). This difference in resolution may be due to the amplicon length of the 12S primers, which was 70 bp in our study but 100 bp in Thomsen et al. (2016). Future eDNA studies should use several loci to reach the highest possible taxonomic resolution.

Our eDNA analysis revealed relatively few cephalopod taxa when compared with, for example, the eastern Atlantic (Merten et al., 2021; Visser et al., 2021). Although the Arctic has a relatively low cephalopod diversity (Xavier et al., 2018), some taxa may not have been detected due to the underrepresentation of Arctic species in our database. Most Arctic cephalopod species are octopuses and sepiolids. However, the *Ceph18S* primer fails to amplify octopus DNA (de Jonge et al., 2021). For instance, the cirrate octopus *Cirroteuthis* sp. is regularly observed on in situ video from the Arctic, including the Fram Strait (Stauffer, 2022), but was not detected with the *Ceph18S* primer.

We detected eight dubious cephalopod and three dubious fish taxa. None of them are known to occur further north than 68°N or are Pacific species. We suspect some dubious taxa to be misassigned to closely related species due to, for example, the absence of the correct species in our reference database. Future efforts should aim to complement reference databases by collecting voucher specimens and by barcoding existing voucher specimens for different marker genes as database gaps hamper eDNA species assignment interpretation (Elbrecht et al., 2017; Kwong et al., 2012). Another reason for dubious detections is predators that may distribute eDNA via defecation (Taberlet et al., 2018). All dubious taxa except of *Chelidonichthys* sp. belong to families that occur in the diets of cetaceans which migrate into the Arctic from the Atlantic (Anderwald et al., 2012; Clarke et al., 1993, 1976; Clarke, 1996; Clarke & Kristensen, 1980; Clarke & MacLeod, 1980; Pierce et al., 2004), In addition, most dubious taxa were represented in less than 10% of the sequencing reads and typically in only one of the three biological replicates. The contrasting read and detection frequencies support the hypothesis that dubious eDNA detections stems from predator feces and not from cephalopods or fish that have changed their distribution. The above discussed potential range expansions for which eDNA was only detected at one station during one cruise and in low read numbers (*Histioteuthis* sp. and Histioteuthidae as well as *Thunnus* sp.) may also result from predator feces. Detectability of taxa with eDNA analysis can be increased by combining multiple primers to target different genes, circumvent primer bias, increase taxonomic resolution, and decrease the likelihood for false negatives. While primers targeting

nuclear rRNA genes (as used in this study for cephalopods) provide a broad taxonomic coverage, the taxonomic resolution is often lower than for mitochondrial rRNA genes (as used in this study for fish; Deagle et al., 2014). Accumulation plots for the number of sequencing reads and number of detected cephalopod taxa also showed that the sequencing depth and number of stations sampled was not sufficient to capture the total cephalopod diversity of the sampled ecosystem. Therefore, a higher sequencing depth and larger sample size may allow to detect more rare cephalopod species.

The nekton biodiversity of the Arctic Ocean faces significant global changes which likely resonate through the foodweb and place Arctic ecosystems at risk. Biodiversity monitoring is needed to detect changes in ecosystem structure, functioning, and ultimately the provision of ecosystem services. We showed that despite limitations, eDNA metabarcoding can be utilized as an efficient tool to provide the required information in the monitoring of nekton in the rapidly changing Arctic Ocean.

AUTHOR CONTRIBUTIONS

HJH conceived the study. VM, HJH, OP, TB, and TBHR planned the study. VM collected the samples. VM, JF, JS, and JBS conducted the laboratory work. KM contributed data. VM analyzed the data with contributions from TB and HJH. VM and HJH wrote the manuscript. OP, TB, TBHR, JF, JS, KM, and JBS critically reviewed the manuscript. All authors contributed to the manuscript and approved the submitted version.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The raw sequencing data are available on DRYAD (https://doi.org/10.5061/dryad.5qfttdz92). The metadata of the raw sequences and the tag files are found in the supplementary material. Any enquiries should be directed to the corresponding author.

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SUPPORTING INFORMATION

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

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