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Research Article

Community structure and range shifts in Arctic marine fish under climate change

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Arctic marine ecosystems are rapidly transforming due to climate change. Warming temperatures and shrinking sea ice are enabling boreal fish to expand northward, possibly disturbing cold-adapted Arctic species assemblages. Species range shifts have been documented in the Bering and Barents Seas, raising concerns about ecosystem restructuring. Range shifts are especially difficult to detect in the Arctic due to sparse and inconsistent data. Here, we studied fish composition from eDNA water samples taken in East Greenland, Svalbard, the Barents Sea, and the Kara Sea during the TOPtoTOP and Arctic Century expeditions. We examined the environmental drivers of fish community structure using global dissimilarity models. We calculated the decadal rate of temperature change to identify the fastest-changing areas. We compared fish detections from eDNA with published historical records for the Kara Sea to assess possible range expansions. We found that temperature was the main factor influencing the taxa turnover of fish communities, with Gadidae and *Liparis* sp. driving the greatest compositional differences. Over the past 30 years, temperatures increased by 0.2 to 0.6°C per decade at our study sites, with the highest increases in western Svalbard and the lowest in the eastern Kara Sea. Despite the apparent dependence on temperature, we identified only one species detected outside its known latitudinal range, and five species in the Kara Sea with recent occurrences or representing an extended distribution. Our study suggests that temperature, the main driver of fish community assembly, is increasing rapidly in the Arctic, and a few species have likely already shifted recently, or at least their detections are new in some areas. While these detections cannot be definitively linked to range shifts, our results highlight the need to improve monitoring of high-latitude fish communities to detect and predict future ecosystem changes.

Keywords: Arctic, climate change, community, eDNA, Kara Sea, range shift, trawling

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Introduction

Arctic marine ecosystems host locally adapted fish communities to unique environmental conditions (Callaghan et al. 2004, Mecklenburg et al. 2011). Sea temperature at these high latitudes can be near-freezing year-round, with extreme seasonal and spatial variability in sea ice coverage and daylight duration. Although these communities are shaped by long-term evolutionary processes, they now face rapid environmental changes (Mecklenburg et al. 2011). Arctic seas have warmed more than twice the global average, and poleward migration of cold-adapted species is constrained by the deep ocean basins beyond the continental shelf (Cai et al. 2021, Rantanen et al. 2022). Simultaneously, boreal species are moving northward, creating novel competition and predation pressures (Johannesen et al. 2020).

Despite their ecological and economic significance, many Arctic shelf regions remain under-sampled, notably due to persistent sea ice and logistical constraints limiting knowledge of the distribution of Arctic fish assemblages. In the Kara Sea, adjacent to the warmer Barents Sea where sea ice persists much of the year, successful trawl surveys are rare, especially at the highest latitudes (Dolgov 2013). Some northernmost areas of the shelf were trawled for the first time in the early 2000s (Dolgov 2013), despite being on the forefront for boreal species range expansion due to the proximity to the Barent Sea. Documenting current fish biogeography is therefore critical for detecting impacts of ongoing environmental changes and understanding how ecosystem services may be impacted (Huntington et al. 2020, Cheung et al. 2021). Species checklists from the Arctic suggest that the Kara Sea hosts Arctic assemblages with lower richness than the adjacent Barents Sea shelf (Lynghammar et al. 2013), and highlights the importance of current influence. The shelf around Svalbard is a transition zone between Atlantic and Arctic water origin, which influences fish assemblages (Bergstad et al. 2018).

Climate change is already affecting Arctic marine fish communities. Warming waters and diminishing sea ice are facilitating the northward movement of boreal species, which can disrupt ecosystem structure and alter species interactions (Kortsch et al. 2015, Pecuchet et al. 2020). Such shifts have been documented in the Barents Sea, where Atlantic and Arctic water masses meet (Oziel et al. 2016): boreal species like Atlantic cod and haddock have expanded northward, while Arctic species (such as polar cod and Arctic staghorn sculpin) lost their southernmost range (Fossheim et al. 2015, Misund et al. 2016, Dupont et al. 2020, von Biela et al. 2023). During unusually warm years, Atlantic cod has intruded into the Kara Sea (Dolgov 2013). Similar poleward shifts have occurred in the Bering Sea, where species such as walleye pollock and Pacific cod have tracked rising temperatures (Stevenson and Lauth 2019). These shifts can restructure Arctic ecosystems, as boreal fish communities tend to be larger, more mobile, and more piscivorous than the Arctic assemblages dominated by small benthic fishes (Wiedmann et al. 2014, Frainer et al. 2017). Warming seas may favour boreal species over Arctic-adapted ones and alter the ecosystem dynamics, but our ability to detect such range shifts is limited by coarse or inconsistent baseline data across much of the Arctic shelves.

Most knowledge on Arctic fish communities comes from fisheries or scientific trawl surveys (Christiansen et al. 2014). However, molecular tools like environmental DNA (eDNA) analyses can complement traditional sampling by accessing areas that are challenging to trawl and avoiding destructive impacts on benthic habitats (Eigaard et al. 2017, Westgaard et al. 2024). Environmental DNA metabarcoding requires only sampling litres of seawater followed by laboratory and bioinformatic processing (Deiner et al. 2017) and can strengthen biogeographic documentation and track species range shifts (Mathon et al. 2023). In polar waters, eDNA metabarcoding has already proven effective in characterizing fish communities in Greenland and Svalbard (Merten et al. 2023, Schiøtt et al. 2023). It generally recovers similar taxa as trawling while detecting additional pelagic species, although it can miss some locally rare species and flatfishes (Veron et al. 2023, Guri et al. 2024, Rehill et al. 2024). eDNA metabarcoding thus provides an efficient method for sampling in Arctic areas with limited access.

In this study, we used eDNA metabarcoding across a large spatial gradient in the Arctic to test hypotheses about the environmental drivers of fish community structure and the influence of climate change on species distributions. We addressed the following questions: 1) What are the main environmental factors structuring the composition of the Arctic fish communities? 2) Do these environmental drivers similarly structure the fish communities of the Kara Sea? and 3) Do we currently detect species outside their historical documented ranges? We hypothesize that climate-related factors are the primary drivers of Arctic fish community structure and are similarly influencing communities in the Kara Sea. We further hypothesize that several fish species would be detected beyond their historically documented ranges, particularly in areas that have experienced the most significant recent warming. By integrating molecular occurrence data with environmental variables and historical species records, we aim to better understand the environmental processes shaping Arctic fish communities and evaluate potential signs of recent climate-driven spatial redistribution.

Material and methods

Study area and fish eDNA sampling

A total of 89 eDNA water samples were collected over a large range of latitude (65°69′–82°82′N) and longitude (23°69′E–103°85′W), and spanning a gradient of environmental conditions (Supporting information). The TOPtoTOP Expedition (42 samples, 42 sites) sampled surface water in summer 2020 and 2021. Samples were collected from the Pachamama expedition sailboat using a peristaltic pump to filter ~ 30 l of water per sample. The Arctic Century Expedition collected 47 samples from 28 sites around the northern part of the Kara Sea on board the icebreaker R/V Akademik Tryoshnikov. Both surface (n = 21) and deeper water (n = 26) samples were collected. Deep water samples were taken as close as possible to the seafloor, either with a submersible peristaltic pump (~ 30 l) or with several 10 l Niskin bottles if the depth was greater than 200 m, due to the pump's pressure limitations. Surface water samples were collected using the same submersible pump. Filtered volume with the Niskin bottle ranged from 60 l (6 bottles) to 120 l (12 bottles). Due to pump malfunctions, a few samples between 0 and 200 m were also sampled using the Niskin bottle procedure. Sampling depths ranged from 0 to 2149 m. All samples were collected with a 0.2 µm filtration capsule and disposable sterile or bleached tubing. DNA was preserved with a conservation buffer (CL1, SPYGEN).

eDNA extraction, amplification, sequencing and data processing

DNA extraction, amplification and sequencing were performed following Polanco et al. (2020). Briefly, DNA amplification was performed following a modified protocol of the NucleoSpin Soil extraction kit (MACHEREY-NAGEL) (Supporting information). Then, DNA amplification was carried out with the 12S teleo primer pair (Valentini et al. 2016), with 12 PCR replicates per sample, all individually tagged. Eight libraries were prepared using the MetaFast protocol, and sequencing was carried out on a MiSeq Flow Cell Kit ver. 3 (Illumina) 2 × 125 bp. Several negative extraction and PCR controls were amplified and sequenced to monitor potential contamination.

The fish sequence data were processed to generate a list of taxonomic entities (taxa) corresponding to distinct species. We applied a bioinformatic pipeline using the 'OBITools' toolkit ver. 1 (Boyer et al. 2016). Reads were merged using the function *illuminapairend*, demultiplexed using *nsgfilter* (no mismatch allowed) and cleaned using *obiclean* (r = 0.05). Taxonomic assignment was performed using the function *ecotag* on the EMBL reference database (06.2022). We accounted for tag-jump by removing all sequence occurrences below a 0.001 ratio of their total abundance in a given library (Schnell et al. 2015). Data were further cleaned by removing all occurrences below 10 reads. As no fish sequences were found in the negative controls, no further cleaning was necessary. Taxonomic assignments were refined to only keep species likely to occur in the area (e.g. occurring in the ecoregions or in close vicinity based on FishBase maps and GBIF occurrences), downgrading species-level assignments to genus-level or family-level if they are not known to occur in that part of the Arctic (Supporting information). To reduce redundancy, we removed genus- or family-level taxonomic assignments from samples in which conspecific taxa were identified at the species level. This step helped avoid misassignments caused by limited taxonomic resolution of our primers and gaps in the reference database (Supporting information). We then generated the final dataset by merging sequences assigned to the same taxon, summing reads, and performing analyses at the taxonomic level, but only used presence/absence information.

Arctic environmental parameters

We extracted environmental data from the Marine Copernicus service: net primary productivity (NPP), nitrate (NO3), chlorophyll a (chl a) (ARCTIC_MULTIYEAR_BGC_002_005; 2007–2020) and sea surface salinity, sea surface temperature (SST) and sea ice cover (ARCTIC_MULTIYEAR_PHY_002_003; 2007–2020). We averaged values for each parameter over the entire period to build a multi-year average from the monthly-mean products. Seabed depth was obtained from GEBCO (2024) Grid and distance to land from the GMED (Basher et al. 2018).

Large-scale environmental gradients and biogeographical analysis of fish eDNA

We characterized the environmental conditions of all sites using principal component analysis (PCA) from the following parameters: SST, surface salinity, chl a, sampling depth, sea ice cover, and seabed depth. We excluded highly collinear variables to avoid redundancy and improve interpretability of the ordination. To analyse fish community composition, we performed a principal coordinates analysis (PCoA) based on Jaccard dissimilarity, computed from presence–absence data derived from eDNA metabarcoding detections. We assessed the relationship between environmental and biotic patterns by comparing site ordinations from the PCA and PCoA. Additionally, we partitioned total beta diversity into their nestedness and turnover components following Baselga et al. (2023) to quantify the effects of species turnover and richness differences on community variation using the 'betapart' R package. All analyses were done on R (ver. 4.4, www.r-project.org).

To better understand the structure of Arctic fish communities, we quantified the contribution of individual species and sites to overall beta diversity. Specifically, we calculated species contribution to beta diversity (SCBD) to identify taxa driving community turnover, and local contribution to beta diversity (LCBD) to highlight sites with unique community compositions (Legendre 2014) using presence/absence from the R package 'adespatial', function *beta.div*. To explore the environmental drivers underlying these patterns, we used a generalized dissimilarity model (GDM) using the R package 'gdm' (Fitzpatrick et al. 2022). GDM is particularly well-suited for modeling non-linear relationships between environmental gradients and community dissimilarity. We included non-collinear predictors (variance inflation factor < 5): sea surface temperature (SST), salinity, chl a, sampling depth, and seabed depth. Five samples were excluded from the GDM analysis due to missing environmental data.

Depth gradient analysis of eDNA metabarcoding in the Kara Sea

Focussing on the Kara Sea, we explored the drivers of fish community assembly at a more local scale, leveraging in situ CTD (conductivity, temperature, depth) measurements with extra sensors (chl a) obtained across the full depth gradient during the Arctic Century Expedition. The research vessel trajectory was split into four transects from 300 to 1000 km sections. For each transect, we extrapolated the temperature value obtained from CTD drops using R by applying a multilevel B-splines method available in the 'MBA' package from the methods of Lee et al. (1997). Next, we mapped 1) the thermal and 2) depth range of all detected species by eDNA metabarcoding from our in situ CTD measurements. We then modelled the drivers of fish community dissimilarity with environmental parameters measured at the scale of the Kara Sea using a GDM after controlling for multicollinearity with the following set of variables: temperature, salinity, chl a, geographic distance between pairs of sites, sample depth, seabed depth. We ran a separate GDM model focussing solely on deeper samples (> 60 m) as the environment is more homogeneous than at the surface.

Climate change analysis for SST and sea ice cover

To understand the past environmental stressors at the scale of our study area in the Arctic, we calculated the trend of SST change using the ARCTIC_MULTIYEAR_PHY_002_003 dataset, from monthly mean average (1991–2021). We computed the temperature change rate using the *temporalTrend* function from the 'climetrics' R package (Taheri et al. 2024), which computes the slope of a variable variation across time. We computed the metric for each 12.5 × 12.5 km cell from 1991 to 2021 (monthly average). We used the same methodology to compute the sea ice cover change rate over 1991–2021 from the same dataset. We also computed the distance-based velocity of climate change for SST for each 12.5 × 12.5 km cell using the 'climetrics' R package (dvelocity; Taheri et al. 2024), using 1991/2001 as baseline and 2010/2020 as the second period from monthly averages. This metric quantified the rate at which isotherms shift spatially over time (in km year^{-1}), representing how fast species should move to remain in similar temperature conditions. Then, we mapped each eDNA sampling site to its value of SST change rate, sea ice cover change rate or SST velocity change.

Comparisons of fish eDNA with historical occurrence records

We used historical records of fish occurrences to extract the known latitude range of the species we detected in the present analysis with eDNA metabarcoding. Due to the lack of available historical data in the Kara Sea region, we splitted the analysis and compared it separately with data from the literature to assess whether any taxa were 1) new to the Kara Sea, 2) newly detected in the Kara Sea, 3) detected in new areas of the Kara Sea.

For the latitude comparison, we used two occurrence sources: 1) the OBIS global database (Ocean Biodiversity Information System) from 1900–2023, and 2) demersal fish data from trawl ecosystem surveys in the Norwegian waters of the Barents Sea and Svalbard (Johannesen et al. 2021, Prozorkevich and van der Meeren 2022) from 2004–2021 in August–September (Supporting information). All taxa were also compared to the species occurrence information given in two different 'Atlas of the Barents Sea fishes' (Wienerroither et al. 2011, 2013), which include occurrences from the Russian part of the Barents Sea. As those records are only from PDF maps, no distribution could be easily and reliably extracted. For every species which we detected outside their known latitude range, we manually checked the maps for any detections in higher latitude and flagged these species. For higher than species-level assignments, we compiled the data for all species of the genus to be conservative. Family-level assignments were not assessed due to the high number of species it could represent. For the Kara Sea comparison, we used the latest available English checklist from Dolgov (2013) to extract whether the species were known in the area and since when, and used maps provided in Dolgov et al. (2018) to compare the distribution extent of known species. As some species were missing in the earlier reference but present in the most recent one, we would only consider a taxa new in the area if absent in both checklists.

Results

Fish taxa and richness identified by eDNA metabarcoding

Our eDNA metabarcoding assay generated 25 364 659 reads across 89 samples (Supporting information), from which we identified 48 fish species or taxa (Methods). The family Gadidae was the most frequently detected taxa, present in 84% of the samples (75/89), followed by *Liparis* sp., detected in 52% of samples (46/89). Due to the limited taxonomic resolution of the teleo marker and low interspecific genetic differentiation within the family, Gadidae detections could correspond to at least 12 species (*Gadus morhua*: Atlantic cod, *Gadus chalcogrammus, Melanogrammus aeglefinus*: haddock, *Boreogadus saida*: polar cod, *Arctogadus glacialis*: ice cod, *Gadus macrocephalus, Gadus ogac, Merlangius merlangus*: whiting, *Microgadus proximus, Pollachius virens*: saithe, *Eleginus gracilis, Merluccius australis*). Most of the reads were assigned to Gadidae (18.1% of total reads, 4 603 165) and *Mallotus villosus* (capelin) (17.5% of total reads, 4 439 759). On average, 4.12 species were detected per sample, with the highest diversity recorded (19 species) from a site in Iceland.

Environmental gradients and biogeographic patterns of fish eDNA

We characterized the large-scale environmental gradients across our Arctic study area using averaged surface water parameters. PCA revealed a primarily latitudinal structuring along the first axis, with northern sites generally exhibiting lower SST, lower salinity and higher sea ice cover compared to southern sites (Fig. 1A, B). The sites in East Greenland (70°N) exhibit more northern characteristics, with similar environments as sites from 75°N. Around Svalbard, the south-west side shows more Atlantic water influence, with higher temperature and lower sea ice cover with a transition towards more Arctic-influenced waters in the north-east and west, exhibiting lower temperature and higher sea ice cover. In the Kara Sea, sites are distinguished by their higher sea ice cover and lower SST, reflecting Arctic conditions. They are

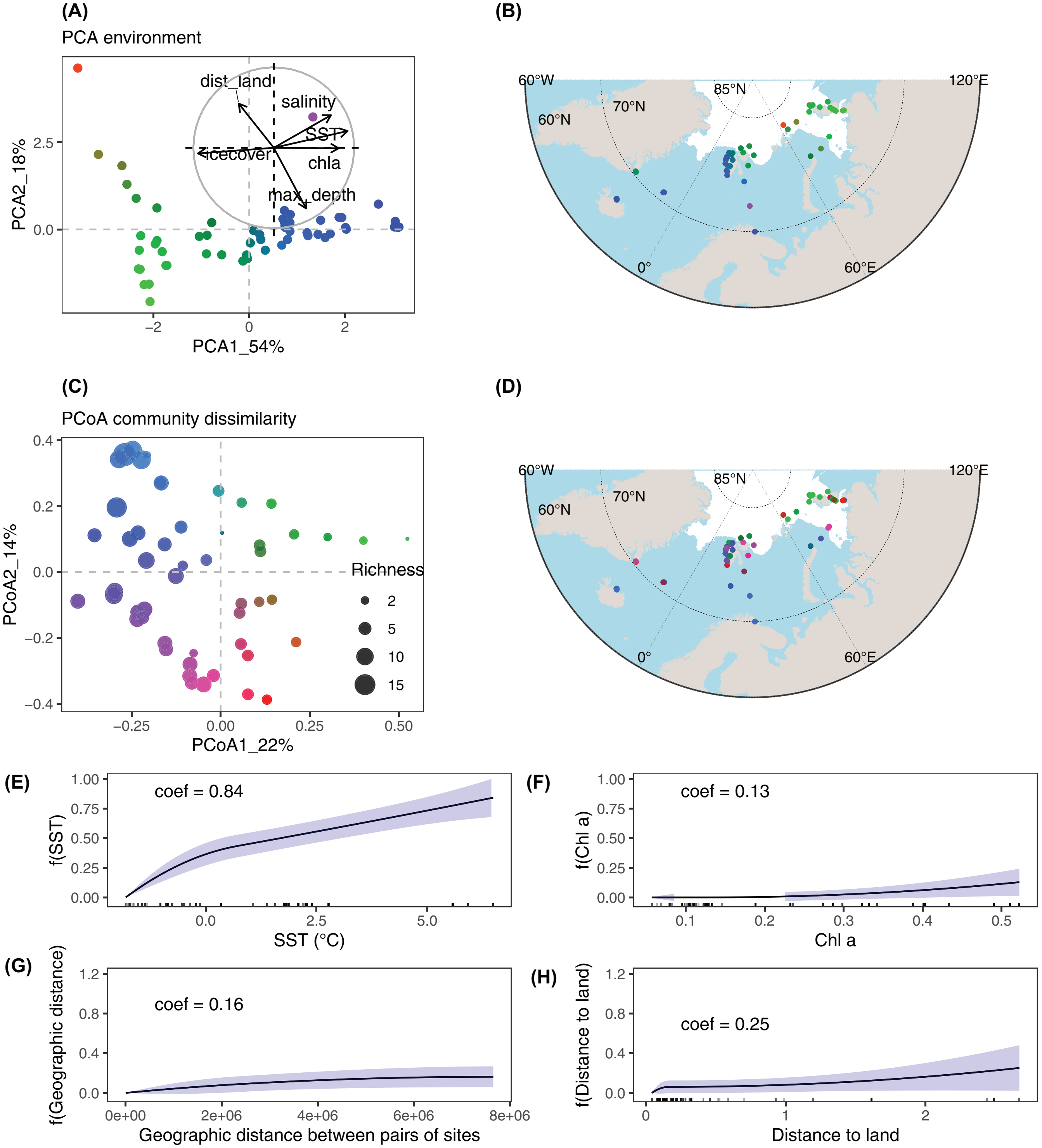

Figure 1. (A) Ordination of sites based on multi-year average of environmental parameters using a PCA. (B) Map of corresponding PCA ordination showing sea ice extent (mean of July 2021). (C) Ordination of sites based on their total community dissimilarity (based on eDNA) using a PCoA. (D) Map of the corresponding PCoA ordination and (E–H) individual spline extracts of GDM modelling for the corresponding environmental values, non-significant variables not shown, with intervals from bootstrapping 500 times excluding 30% of samples. Colors represent the position of samples in the ordination. All plots consider only surface samples.

further differentiated from Svalbard along the second PCA axis, with deeper seabed depth or greater distance to land.

Fish community composition from surface-water eDNA metabarcoding shows a clear spatial structure with a strong latitudinal influence, especially west of 60°E longitude (Fig. 1C, D). The fish community in eastern Svalbard is a transitional fish community, representing a blend of northern and southern species assemblage, although the signal is patchier and the transition less clear than for the environmental conditions. The northernmost sites across the study area have distinct community features, hosting species such as *Icelus spatula* and *Gymnocanthus tricuspis,* which were exclusively detected in east Greenland, northern Svalbard and the parts of the Kara Sea. Fish communities in the Kara Sea have some similarities to northern Svalbard, but sites in the Kara Sea are dissimilar from all other sites, although they are closer to northern sites compared to southern boreal sites in Iceland and northern Norway. This differentiation is primarily driven by the nestedness component of the beta diversity (Supporting information) rather than turnover, indicating that the Kara Sea communities generally represent a subset of taxa found in northern areas, rather than hosting a completely distinct assemblage. This pattern is especially true for the northernmost part of the Kara Sea, where taxa richness is low and typical communities detected are mainly composed of Gadidae. Mean alpha diversity by site is lower in the Kara Sea than in Svalbard (Supporting information), yet some species were only detected in the Kara Sea such as *Paraliparis* sp., *Ulcina olrikii*, and *Coregonus* sp., suggesting the presence of regionally distinct species within the more broadly detected northern species assemblage.

Species contribution to beta diversity (SCBD) analysis identified Gadidae, *Liparis* sp., *Mallotus villosus*, Cottidae and *Gymnocanthus tricuspis* as the taxa contributing most strongly to overall compositional dissimilarity (SCBD > 0.075; Supporting information). At the site level, local contribution to beta diversity (LCBD) scores were highest in sites from eastern and western Kara Sea, eastern Svalbard and northern Iceland, indicating that these locations host more distinct assemblages relative to the regional dataset (LCBD > 0.025; Supporting information). To investigate which environmental parameter might explain the dissimilarity of the fish community detected from eDNA, we modelled it using GDM (Fig. 1E–H; non-significant relationship not shown). Overall, the percentage of explained deviance was 16.1% and the most important parameter driving dissimilarity was the SST. Other important parameters were the chlorophyll concentration, distance to land, and pairwise site distance. We observe a stronger slope from the GDM model around the coldest temperature (−1.8–0°C) compared to other temperatures (e.g. 0–2°C or 2–4°C).

Environmental structuring of the Kara Sea fish communities

At the scale of the Kara Sea, environmental conditions varied along spatial gradients, with SST generally higher in the west compared to the east. Salinity levels were influenced by freshwater inputs from river discharge and sea ice melt, while bottom water temperatures were more uniform along the shelf (Fig. 2). To assess how these environmental factors influenced fish community dissimilarity based on eDNA metabarcoding, we modelled it using GDM (Fig. 2). The model explained 15% of the observed dissimilarity. In situ temperature was the most important predictor (coefficient = 0.68), followed by sampling depth (0.47) and salinity (0.27), although salinity showed greater uncertainty. Chlorophyll-a concentration had no detectable effect, while seabed depth and geographic distance contributed less (coefficients up to 0.25). Focussing the analysis solely on deep samples (depth > 60 m) explained 35% of dissimilarity and showed that depth and salinity were the most important predictors, together with geography (samples further away were more differentiated) (Supporting information).

Depth gradient of fish eDNA in the Kara Sea

We analysed Kara Sea environmental profiles along four transects to integrate temperature over the water column (Fig. 3). Transects crossed topographic features like the Saint Anna and Voronin troughs, where warmer intermediate waters (1–3°C) were observed at greater depths compared to surrounding shelf areas. Temperatures generally decrease with depth, reaching −1.5°C. Transects 3 and 4 showed more uniformly cold waters (−1°C), except for isolated deeper pockets of warmer water off the shelf. Freshwater influence was evident through low surface salinities (down to 11 PSU), particularly in T1 and T4, likely reflecting riverine input and sea ice melt (Supporting information).

The detected species richness from eDNA metabarcoding along these transects indicates a higher diversity closer to the bottom in deeper waters (Supporting information) compared to the surface layer, where we sometimes did not detect any species. Two surface sites with a low salinity yielded 0 detected species within T4. The highest diversity was found overall along T4 with a site harboring nine species (26 m depth, −1.2°C) and along T1 with two sites harboring eight species (20 and 41 m depth, 0.49 and −0.7°C, respectively). The only detection of the whitefish *Coregonus* sp. was at T4_9 both at the surface and bottom (26 m) with a salinity of 14 and 33 PSU. Few species are found across both surface and deeper waters (> 1000 m), including *Paraliparis* sp., *Amblyraja* sp., and at least one species from the species complex assigned to the Gadidae family (Fig. 4A, B). The threadfin seasnail *Rhodichtys regina*, a deep-sea fish species, was the only one detected exclusively at 2000 m depth.

Climate change analysis and comparison of fish eDNA with historical records

SST temporal trend ranged from −0.37 to 0.94°C decade^{-1} above 50°N, with our surface sampling sites located in areas with temperature change ranging from 0.02 to 0.67°C decade^{-1} (Fig. 4, Supporting information), corresponding to sites in the eastern Barents Sea bordering the Kara Sea (lowest) and western Svalbard (highest). The distance-based velocity of SST change ranged from −36 to 249 km decade^{-1},

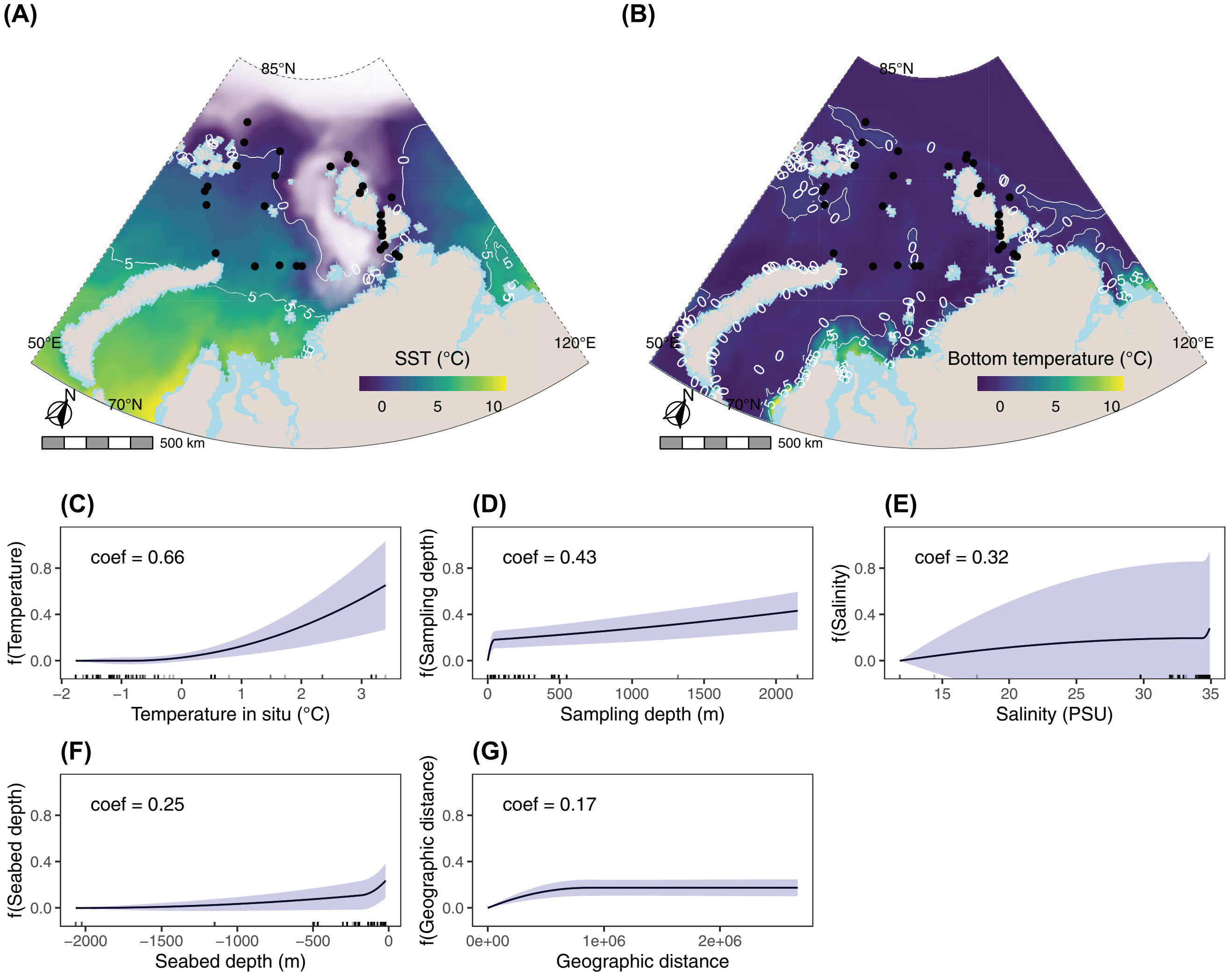

Figure 2. Local map of the Kara Sea eDNA sites with color and isolines representing temperature with (A) SST (mean for August 2021 from model-derived product) and sea ice cover in white with transparency corresponding to the mean sea ice cover (August 2021 from model-derived product) between 0 (no sea ice) and 1 (covered by sea ice); and (B) bottom temperature (mean for August 2021 from model-derived product) and (C–G) individual GDM I-splines from the GDM showing the effect of local environment on the modelled dissimilarity, using in situ measurements for temperature, depth and salinity with intervals from bootstrapping 500 times excluding 30% of samples.

with values of 15 to 225 km decade^{-1} for our sampling sites (Supporting information). Sea ice loss was highest in eastern Svalbard and the western Kara Sea (Supporting information). As environmental parameters are major drivers of community composition, we explored whether any detected species by eDNA metabarcoding was found outside of its known latitudinal range (Fig. 4). Over all our samples excluding the Kara Sea, one species was found at a potentially higher latitude than previously reported: the basking shark *Cetorhinus maximus*. However, it was likely detected in slightly higher latitude previously as reported in the 'Atlas of the Barents Sea fishes', but the only information is a visual observation from south of Bear Island without GPS coordinates (Wienerroither et al. 2011). Focusing only on the Kara Sea samples (surface and deep samples), we detected eight species outside of their known latitude range. Due to the lack of spatially-explicit public records for the Kara Sea preventing a fair assessment for a range shift analysis, we compared our detections to broader Kara Sea checklists (Dolgov 2013, Dolgov et al. 2018). We found no species previously never recorded in the Kara Sea, yet some species were not mentioned in the earlier checklist (e.g. *Anarhichas* sp., *Paraliparis* sp.; Fig. 4). Three taxa (*Reinhardtius hippoglossoides*, Myctophidae, *Cottonculus microps*) were previously recorded but only recently (early 2000s), and two taxa were detected in another part of the Kara Sea compared to previous record (*Clupea*, *Anarhichas*). For species detected within their known latitude range, most were detected at the edge of their known higher latitude, such as *Triglops* sp. (78.69°N vs 80.24°N) or *Cyclopterus lumpus* (80.00°N versus 80.60°N).

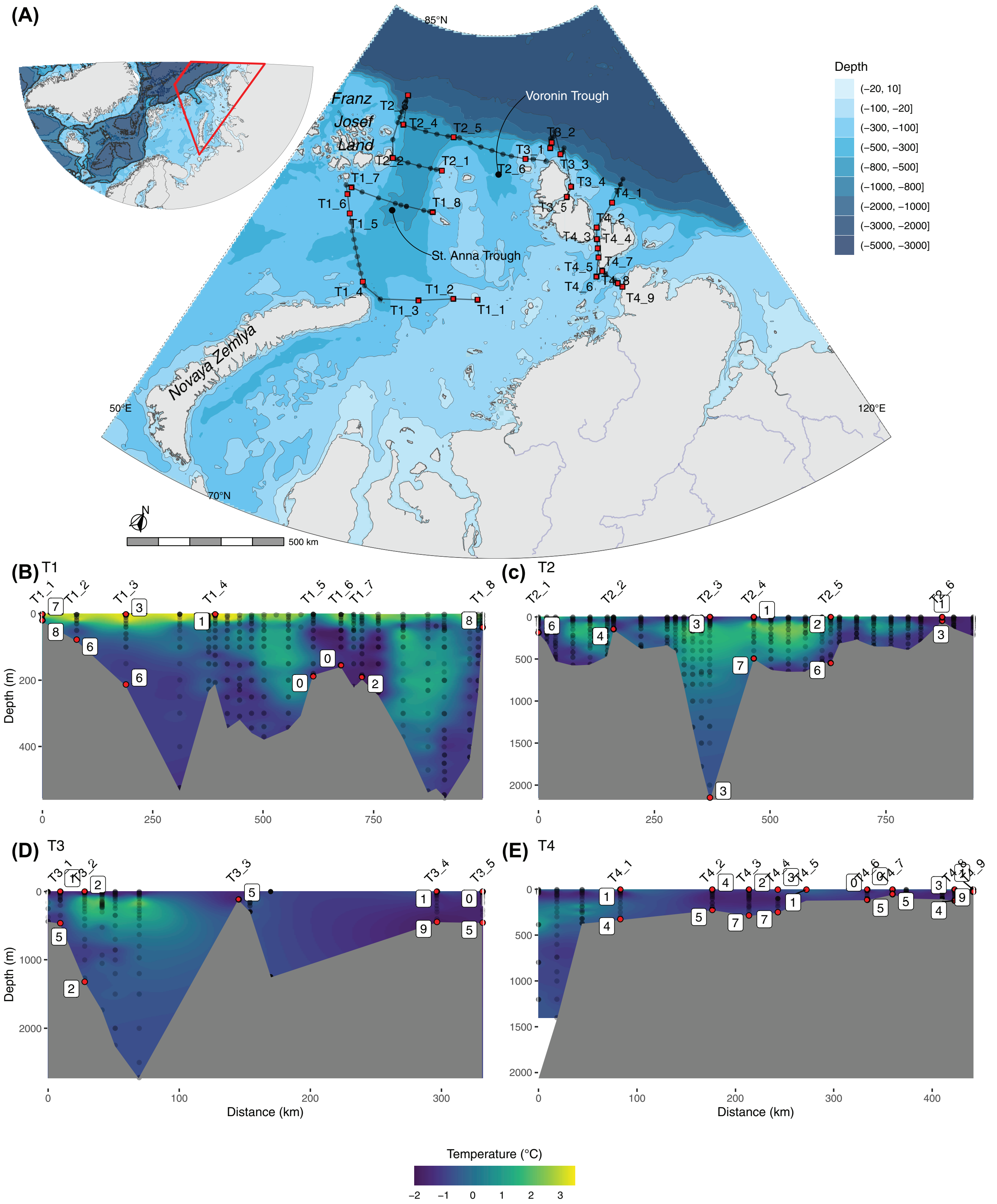

Figure 3. Sampling map (A) and abiotic characterization of the Kara Sea area for temperature for Transects 1 to 4 (B–E). Black transparent dots are the temperature measurements from the CTD (conductivity, temperature, depth) instrument, red dots eDNA sampling site, labels showing the number of species detected.

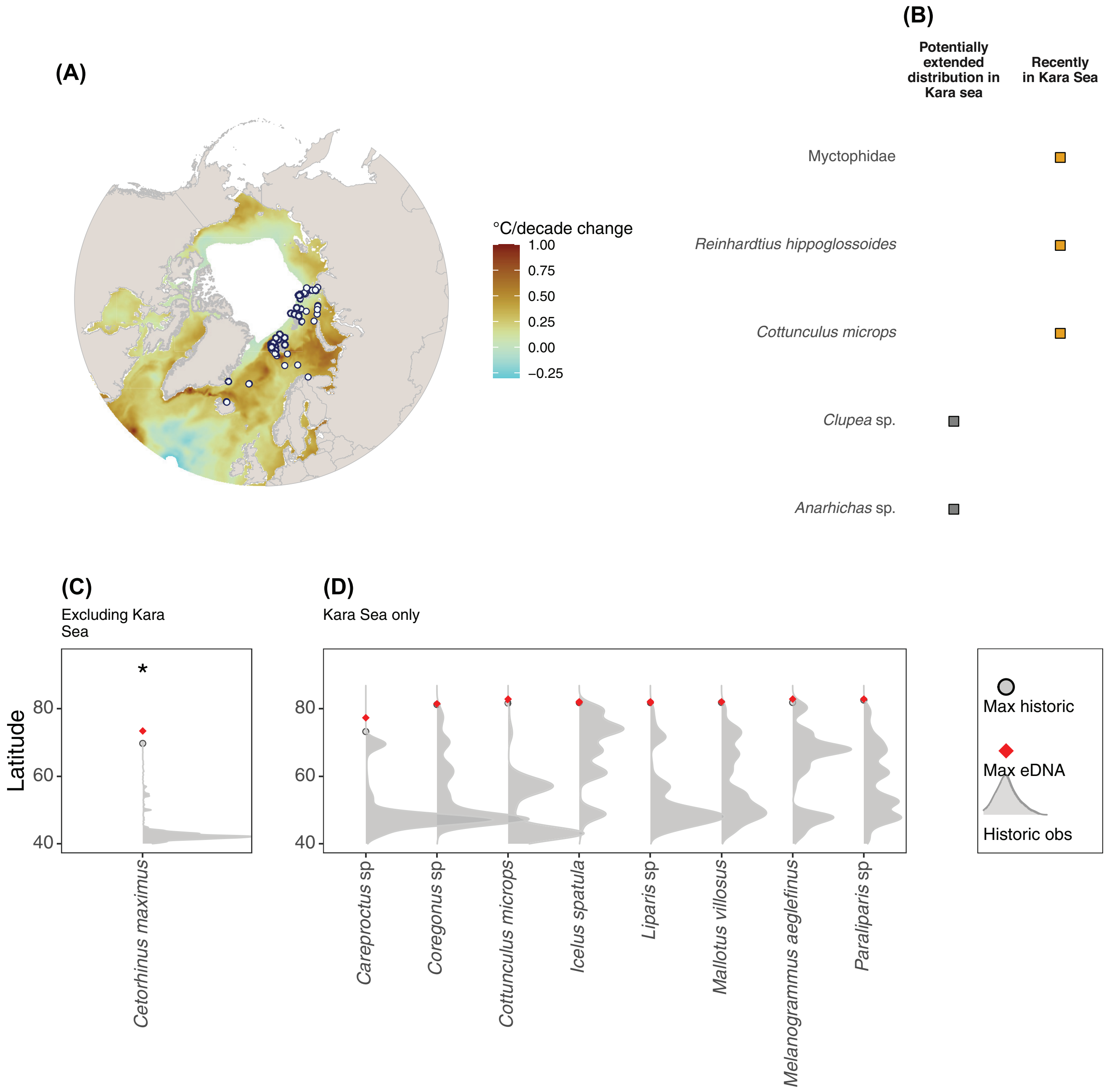

Figure 4. (A) Trend of SST change in °C decade^{-1} for the period 1991–2021 excluding areas with an average of more than 90% sea ice cover (mean over 1991–2021) and corresponding eDNA sampling points in white and (B) indication for the Kara Sea ecoregion only whether the species were recently detected in the Kara Sea (only from the 2000s) as per Dolgov et al. (2018) or representing potentially extended distribution based on known occurrences from maps of Dolgov et al. (2018), (C) range shift analysis with latitude of historical observations compared with latitude of eDNA occurrences from the present study (B) excluding the Kara Sea and (C) exclusive to the Kara Sea. The * sign indicates species for which previous detections were found at higher or similar latitudes than our eDNA samples but only within written records of 'Barents Sea ATLAS' and not present within any georeferenced database used in the paper.

Discussion

Large areas of the high-latitude Arctic shelf remain under sampled mostly due to challenging accessibility, limiting our understanding of the consequences of warming temperatures on fish biodiversity. Our results demonstrate that temperature is the most important environmental factor structuring Arctic fish communities. At the more local Kara Sea scale, temperature also drives community structuring, but depth is also important. Contrary to many other places, poleward migration to track colder temperatures will quickly be limited for Arctic species as increased seabed depth outside the Arctic shelf constrains species establishment. Temperature change was estimated to be up to 0.6°C decade^{-1} in our sampled areas, suggesting strong environmental changes in the last years. While only one species was detected outside its previously recorded latitude range, we found five species in the Kara Sea that represent either recent arrivals or broader distributions than previously documented.

Fish communities are structured along environmental gradients across our study area. In the Barents Sea, we recovered expected patterns of diversity, with 'Atlantic' influenced assemblages off western Svalbard separated from 'Arctic' influenced assemblages in north-east Svalbard or the Kara Sea (Fossheim et al. 2015, Johannesen et al. 2021). Currents strongly influence environmental conditions over the area, with Arctic water flowing as low as 70°N in East Greenland while Atlantic water flows as high as 75°N in the Barents Sea depending on the position of the polar front (Oziel et al. 2016), representing an oceanographic boundary separating the two water masses (Atlantic water; warm and saline and Arctic water, cold and fresh). This environmental feature is known to split the fish community into a warm-affinity assemblage (south of the front) and cold-affinity assemblage (north of the front) (Fossheim et al. 2015, Johannesen et al. 2021). The Kara Sea hosts an overall low species richness, corresponding mainly to a subset of other Arctic communities with assemblages dominated by small Arctic fish, a pattern potentially driven by higher sea ice cover and lower productivity exerting strong environmental filtering (Hanzlick and Aagaard 1980, Schauer et al. 2002, Demidov et al. 2018, Terhaar et al. 2021). However, most of the shared detection of Gadidae likely reflects different species depending on the region, and a better taxonomic resolution would likely further differentiate our sites. A similar pattern is observed in elasmobranchs, with up to 18 species recorded in the Barents Sea compared to only two species in the Kara Sea (*Amblyraja hyperborea* and *Somniosus microcephalus*) (Lynghammar et al. 2013). The structure of fish communities over the Arctic shelf shows how environmental filtering shapes Arctic fish assemblages, with regions like the Kara Sea representing environmental extremes that currently limit species richness, but fast changing conditions could disturb these patterns in the next decades.

At the scale of the Kara Sea, conditions are not homogeneous, and temperature is also the main driver of fish assemblages. SST shows a clear west-east gradient with eastern areas being colder and with higher sea ice coverage. Species richness overall is low, especially in surface water with mostly Gadidae, which fits previous knowledge from trawling: 97% of the biomass was represented by the polar cod *B. saida*, mainly juveniles (Dolgov et al. 2009, David et al. 2016, Antonov et al. 2017). Juvenile polar cod seem to depend on sea ice coverage and less sea ice has been linked with low recruitment (Huserbråten et al. 2019). The near-constant sea ice coverage of the Kara Sea shelf area likely creates strong environmental filtering in its surface waters, limiting productivity. Salinity variation from sea ice melting or river discharge further constrains the environment for marine fish. The only fisheries in the Kara Sea are dominated by whitefish (*Coregonus* spp.), fished in coastal areas near rivers and estuaries where seaice coverage remains low (Zeller et al. 2011). Deep channels in the northern shelf have warmer waters at intermediate depths as Atlantic water flows in the trough towards the central Arctic basin (Osadchiev et al. 2022), and host distinct assemblages such as Greenland halibut which we only found there, in accordance with trawling studies (Dolgov et al. 2009). We recorded the presence of a deep-water snailfish (*Paraliparis* sp.) along the shelf slope (2149 m) and surface water, which likely reflects the presence of eggs or juveniles. Bottom temperature is relatively homogeneous over the shelf (except the most coastal areas and deep channels), and we showed that depth, salinity and geographic distance are the main drivers of fish dissimilarity in deeper samples. The importance of geographic distance suggests that other, unaccounted variables should also drive community assembly, such as potentially benthos type and biodiversity. Studies indicate that benthos is not homogeneous over the Kara Sea with various sedimentation rates and salinity variation from river run-off notably, which can drive the composition of the zoobenthos on which the fish prey (Jørgensen et al. 1999, Galkin et al. 2015). Part of the Kara Sea's benthos has been categorized as mainly dominated by ophiuroids (Udalov et al. 2024), but recently, snow crab invasion seems to shift the benthos dominance in the western part of the Kara Sea and decrease ophiuroids coverage, the snow crab is not yet well installed in the eastern part (Udalov et al. 2024). The functional consequences of this invasive species spread across the benthic food-web towards fish has not been quantified but can be substantial.

Temperature emerged as the dominant driver of Arctic fish community structure, highlighting its strong potential to disrupt fish assemblages. Over the last decades, the Arctic has experienced among the highest rates of warming globally (Rantanen et al. 2022). We show a spatial pattern in SST warming, with the most important temperature rise occurring in the Barents Sea around Svalbard (up to 1.2°C decade^{-1}). The consequences of this warming are already ongoing: the number of species occurring in Svalbard and the Barents Sea is rising and locally, the abundance of boreal species increases while arctic species decrease (Frainer et al. 2017, Gorska et al. 2023). Some areas of the Kara Sea show lower SST warming rate (e.g. 0.2°C decade^{-1}), but this metric could be biased by sea ice coverage, which is sharply declining over the shelf and leading to major environmental changes despite apparent lower warming rates. While few studies are available in English, Dolgov (2013) report that Atlantic cod *G. morhua* can occur in the western Kara Sea during warm years, such as during the 1930s regional warming anomaly or in the recent decades (Dolgov et al. 2009). Our latitudinal comparison did not reveal apparent range shifts of boreal species in higher latitudes. We detected capelin in east Greenland within its latitude range but with limited occurrences nearby. Interestingly, a documented range shift of capelin is responsible for its recent expansion in southeast Greenland (Pampoulie et al. 2024) from its historical southwest Iceland grounds, following to the loss of summer sea ice associated with increased temperature (+2°C) in southeast Greenland (Heide-Jørgensen et al. 2023). In the Kara Sea, we did not detect new species that would suggest new migrants from the nearby warmer areas that were not previously recorded. Comparisons are hindered by a lack of exploration in some areas of the Kara Sea, where some areas were trawled for the first time in the 2000s (Voronin Trough; Dolgov et al. 2009). Yet, we detected three taxa that were only recently recorded in the Kara Sea (Myctophidae, *R. hippoglossoides* and *C. microps*), which the authors attribute to warming waters allowing more species to enter the Sea (Dolgov 2013). The western Kara Sea is seen as the main gateway for boreal species to enter the shelf (Husson et al. 2024) together with the trough as warmer Atlantic water resides in the channels. It remains challenging to assess whether those species are now yearly residents or only manage to survive in the summer with warmer waters. Two taxa were detected in new areas (Aharchichaidae and *Clupea* sp.; Dolgov et al. 2018) which could highlight a range shift within the shelf or previously missed species. The detection of a *Anarhichas* species (*A. denticulatus*) and other taxa in the Laptev Sea has been linked to the borealization of the Siberian Arctic shelf (Orlov et al. 2023). Here, the shift is eastwards and not solely northwards showing the limits of relying solely on latitude to infer range shifts. Further demonstrating the importance of current influence, occurrences of boreal fish (e.g. *G. morhua*) have been observed in very low abundance in part of the Central Arctic Ocean where Atlantic water flows in proximity to the Farm Strait (Snoeijs-Leijonmalm et al. 2022).

Inferring range shifts from spatial coverage only remains challenging, emphasising the need for large-scale and long-term studies to extract robust trends. While some areas of the Arctic benefit from regular trawling campaigns and openly share the data, others lack standardized monitoring or exploration, and therefore limited information remains publicly available. For eDNA studies focused on the Arctic, future studies should aim to mainly sample the benthic communities instead of solely the surface, as most species are found close to the seabed. Newly developed commercial in situ pumps are promising to sample deeper ecosystems (Muff et al. 2023), but classic Niskin bottles (Merten et al. 2023) are also effective. DNA transport in a cold environment will lower DNA degradation rates, and this raises the concern of the spatial scale of eDNA-based detections and its use to study climate-related range shifts. Dilution and currents in marine environments likely strongly limit the range of DNA transport, with studies highlighting transport only up to a few hundred meters (Murakami et al. 2019) contrary to river systems which can transport DNA for several km (Pont et al. 2018). Depth-related transport (e.g. as part of sinking particles) seems to be very limited as samples from mid or deep water do not integrate the upper levels, as we also observe in our Kara Sea sites (Merten et al. 2023). Abundance-based measures remain of vital importance for range shift analysis, as a few vagrant species are informative but might not indicate a population-level shift (Chaikin et al. 2024). Veron et al. (2023) found that eDNA metabarcoding detected a larger functional breath than trawling and pelagic species but missed more flatfish and could not translate reads to abundance, but Guri et al. (2024) managed to accurately predict biomass using a complex framework with joint statistical modelling from eDNA read and ddPCR quantification. Currently, using eDNA metabarcoding to reliably estimate abundance or biomass remains challenging. We recommend using longer and more resolutive eDNA markers for Arctic communities, as teleo is poorly representing the important Gadidae group, although no marker is expected to reach a perfect resolution (Polanco et al. 2021). This is due to the recent evolution of some families, whose mitochondrial genome is relatively similar (Rabosky et al. 2018, Min et al. 2021). The MiFish marker theoretically provides a better resolution for the Gadidae group and for Arctic assemblages in general, yet its resolution is also limited for some groups such as *Myxocephalus* or *Anarhichas* (Polanco et al. 2021). In our study, this limitation leads to lower beta diversity between locations notably due to the conspicuous and undifferentiated presence of the Gadidae taxa. Despite the limitations of the marker, our large-scale study allowed us to identify spatial organization, as many other groups are not affected by this resolution issue.

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Author contributions

Virginie Marques: Conceptualization (lead); Data curation (lead); Writing – original draft (lead); Methodology (lead); Formal analysis (lead); Writing – review and editing (lead). **Melissa Jaquier**: Investigation (equal); Writing – review and

editing (equal). **Fabian Fopp**: Investigation (equal); Writing – review and editing (equal). **Kari E. Ellingsen**: Investigation (equal); Writing – review and editing (equal); Data curation (equal). **Nigel Yoccoz**: Investigation (equal); Writing – review and editing (equal); Data curation (equal). **Meret Jucker**: Investigation (equal); Writing – review and editing (equal). **Camille Albouy**: Methodology (equal); Writing – review and editing (equal). **Loïc Pellissier**: Supervision (lead); Methodology (equal); Writing – review and editing (equal); Conceptualization (lead); Funding acquisition (lead).

Transparent peer review

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Data availability statement

Demersal fish trawl data from the Norwegian part of the Barents Sea from 2004–2021 are available at https://metadata.nmdc.no/UserInterface. The bioinformatic pipeline code is available: https://gitlab.mbb.cnrs.fr/edna/snakemake_rapidrun_obitools.

Data and codes to reproduce the analysis are available from the EnviDat Repository: https://doi.org/10.16904/envidat.704 (Marques et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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