PDF issue: 2026-06-10

Climate Change Impacts on Antarctic Fish Diversity: A Circumpolar Perspective From eDNA Metabarcoding Assessment

Li, Hai ; Yang, Fang ; Liao, Yuzhuo ; Zhang, Xiang ; Li, Yuan ; Wang, Rui ; Zhang, Ran ; Li, Dong ; Wu, Qianqian ; Lin, Longshan

(Citation)
Diversity and Distributions,31(7):e70053

(Issue Date)
2025-07

(Resource Type)
journal article

(Version)
Version of Record

(Rights)
© 2025 The Author(s). Diversity and Distributions published by John Wiley & Sons Ltd. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

(URL)
https://hdl.handle.net/20.500.14094/0100497644

Diversity and Distributions

RESEARCH ARTICLE OPEN ACCESS

Climate Change Impacts on Antarctic Fish Diversity: A Circumpolar Perspective From eDNA Metabarcoding Assessment

Hai Li[1] | Fang Yang[2] | Yuzhuo Liao[1,3] | Xiang Zhang[1,4] | Yuan Li[1] | Rui Wang[1] | Ran Zhang[1] | Dong Li[5] | Qianqian Wu[6] | Longshan Lin[1]

[1]Laboratory of Marine Biodiversity Research, Third Institute of Oceanography, Ministry of Natural Resources, Xiamen, China | [2]Key Laboratory of Cultivation and High-Value Utilization of Marine Organisms in Fujian Province, Fisheries Research Institute of Fujian, Xiamen, China | [3]College of Ocean and Earth Sciences, Xiamen University, Xiamen, China | [4]College of Oceanography and Ecological Sciences, Shanghai Ocean University, Shanghai, China | [5]Key Laboratory of Marine Ecosystem Dynamics, Second Institute of Oceanography, Ministry of Natural Resources, Hangzhou, China | [6]Graduate School of Human Development and Environment, Kobe University, Kobe, Hyogo, Japan

Correspondence: Qianqian Wu (wuqian1124@yahoo.co.jp; wuqq@people.kobe-u.ac.jp) | Longshan Lin (linlongshan@tio.org.cn)

Received: 14 April 2025 | **Revised:** 10 June 2025 | **Accepted:** 1 July 2025

Editor: Zhonge Hou

Funding: This work was supported by the National Key Research and Development Program of China (2023YFF0611803), the Scientific Research Foundation (2025036) and the 'Cultivating Innovation Team' Program of the Third Institute of Oceanography, Ministry of Natural Resources, the 'Impact and Response of Antarctic Seas to Climate Change' program, Chinese Arctic and Antarctic Administration (IRASCC01-02-02,IRASCC02-02).

Keywords: ecological baseline | eDNA metabarcoding analysis | fish diversity | ichthyoplankton | local reference database | range shift

ABSTRACT

Aim: Recent climate-driven changes in the Antarctic marine environment, marked by regional differences between West and East Antarctica, may alter ecosystem dynamics. As key components of the food web, fish might reflect these changes. This study examines fish biodiversity patterns across four typical Antarctic seas by integrating eDNA analysis with bottom trawl surveys, focusing on biodiversity shifts and range alterations in response to varying levels of climate change exposure.

Location: Four ecologically distinct Antarctic regions: The Adjacent Waters of Antarctic Peninsula (AAP), the Amundsen Sea-Bellingshausen Sea (ASBS), the Prydz Bay-Cooperation Sea (PBCS), and the Cosmonaut Sea (CS).

Methods: During the 37th Chinese National Antarctic Research Expedition, we integrated eDNA metabarcoding (from both pelagic and benthic water layers) with bottom trawl surveys across four regions (AAP, ASBS, PBCS, and CS) to characterise regional fish community.

Results: Environmental DNA metabarcoding and trawl surveys detected 40 and 27 Antarctic fish species, respectively. Environmental DNA proved effective in complementing traditional methods and capturing early life stages, especially with a refined local reference database. Species belonging to the suborder Notothenioidei dominated across all surveyed regions. Ten species exhibited range extensions beyond previously documented distributions, likely reflecting historical data gaps, with the exception of *Patagonotothen* sp.

Main Conclusions: eDNA metabarcoding showed potential for monitoring Antarctic ichthyoplankton. Fish diversity in the four studied seas aligns with the general pattern in the Southern Ocean, while ASBS was identified as a previously overlooked

Hai Li and Fang Yang contributed equally to this work.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2025 The Author(s). *Diversity and Distributions* published by John Wiley & Sons Ltd.

fish diversity hotspot. The southward detection of *Patagonotothen* sp. may signal climate-driven shifts in species distribution. Future research integrating eDNA with interdisciplinary approaches holds promise for advancing the monitoring of climate change impacts on Antarctic marine ecosystems.

1 | Introduction

Over recent decades, the Antarctic marine environment has undergone a series of climate change-driven transformations (Swart et al. 2018), including deep-reaching warming and freshening of surface waters (Haumann et al. 2016), changes in stratification and mixed-layer depth (Pellichero et al. 2017), alterations in ocean circulation (Armour et al. 2016), variation in sea ice duration and extent (Comiso et al. 2017), ice shelf breakup (Liu et al. 2015), oxygen depletion in the water column (Schmidtko et al. 2017) and ocean acidification (Mazloff et al. 2023). These environmental effects directly feedback into the Antarctic marine ecosystem, driving structural changes (Constable et al. 2014; Rogers et al. 2020). Biological responses at the community level may lead to shifts in biodiversity patterns (Gutt et al. 2021), including changes in community structure (Sahade et al. 2015), abundance and distribution (Atkinson et al. 2019) and local species extinctions (Morley et al. 2019). Additionally, climate change has amplified the risk of species invasion as warming temperatures may facilitate poleward movement of alien species (López-Farrán et al. 2021) or expand the habitable range for species that were previously limited (Griffiths et al. 2013), thus further threatening biodiversity (Hughes et al. 2020). Although the impacts of climate change exhibit spatial heterogeneity between West and East Antarctica, with West Antarctica (e.g., Antarctic Peninsula) impacted significantly while East Antarctica is less impacted, continued climate change is expected to affect the entire Antarctica, leading to long-term and profound changes in Antarctic biodiversity patterns (Gutt et al. 2021; Rogers et al. 2020).

As the most species-rich vertebrate group, fish occupy central positions within ecological networks, performing critical ecological functions that reflect ecosystem health and integrity. These attributes position them as effective bioindicators for detecting environmental alterations driven by climate change (Fogarty et al. 2017). Over 360 Antarctic fish species have been recorded in the Southern Ocean (Duhamel et al. 2014; Eastman and Eakin 2021), with the ichthyofauna characterised by high endemism and dominance of suborder Notothenioidei (Eastman 1993). Non-Notothenioid fish mainly belong to deep-sea families such as Zoarcidae, Liparidae, Macrouridae and Myctophidae (Duhamel et al. 2014). Notothenioids dominate demersal fish communities, with species composition varying regionally along latitude, reflecting differences among sub-Antarctic, low Antarctic and high Antarctic zones (Mintenbeck et al. 2012). Pelagic species include neritic and oceanic communities, with Antarctic silverfish (*Pleuragramma antarcticum*) dominating the former and Antarctic lanternfish (e.g., *Electrona antarctica*) dominating the latter (Christiansen et al. 2018).

Antarctic fish play a critical trophic role between lower trophic level organisms and top predators, making them key indicators of climate-driven ecological changes in the Antarctic marine ecosystem (Mintenbeck et al. 2012). However, research on Antarctic fish diversity is often concentrated in areas like the Ross Sea as harsh environmental and logistical constraints limit access to other regions (Griffiths 2010; Hanchet et al. 2013). Traditional capture-based methods are effort-intensive, habitat-selective and potentially disruptive to biodiversity (Liao et al. 2023); these limitations could be further amplified in Antarctica due to remoteness, vast ocean areas, harsh and vulnerable environmental conditions, leaving knowledge of Antarctic fish communities incomplete.

Environmental DNA (eDNA) refers to the total pool of DNA isolated from environmental samples (Pawlowski et al. 2020), including both organismal and extra-organismal DNA (Rodriguez-Ezpeleta et al. 2021). Environmental DNA metabarcoding, integrating eDNA and high-throughput sequencing (HTS) in most cases, has emerged as a promising tool for species detection, offering higher species resolution, broader applicability and lower selectivity than traditional methods (Miya 2022; Yao et al. 2022). By using universal primers, eDNA metabarcoding can simultaneously detect multiple taxa from environmental samples and has proven effective in biodiversity assessments across aquatic ecosystems (Taberlet et al. 2018), such as bay (Djurhuus et al. 2020) and coastal areas (Roblet et al. 2024). It is increasingly recognised as a complementary tool to traditional methods, particularly in the context of climate change (Howell et al. 2021).

In this study, we examined Antarctic fish species in four typical seas contrastingly impacted by climate change: the Adjacent Waters of the Antarctic Peninsula (AAP), the Amundsen Sea-Bellingshausen Sea (ASBS), the Prydz Bay-Cooperation Sea (PBCS), and the Cosmonaut Sea (CS). The objectives were to (1) reveal preliminary spatial fish diversity patterns and assist in establishing ecological baselines for fish communities in the four typical Antarctic regions; and (2) understand potential climate change impacts on Antarctic fish diversity patterns via comparisons among regions with varying levels of climate change exposure.

2 | Materials and Methods

2.1 | Study Areas

During the 37th Chinese National Antarctic Research Expedition (CHINARE-37) cruise (2020-2021), we conducted bottom trawl and eDNA sampling in four representative regions of West and East Antarctica (Figure 1): AAP, ASBS, PBCS and CS. Each region was selected for its unique environmental and ecological characteristics.

The Antarctic Peninsula is experiencing the fastest and most pronounced environmental changes, including ocean warming, ice melting, iceberg scouring and sediment inflow, in the Southern Ocean (La Mesa et al. 2022). The AAP, located near the tip of the Antarctic Peninsula on the Weddell Sea side,

14724642, 2025, 7, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ddi.70053 by Kobe University, Wiley Online Library on [23/09/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

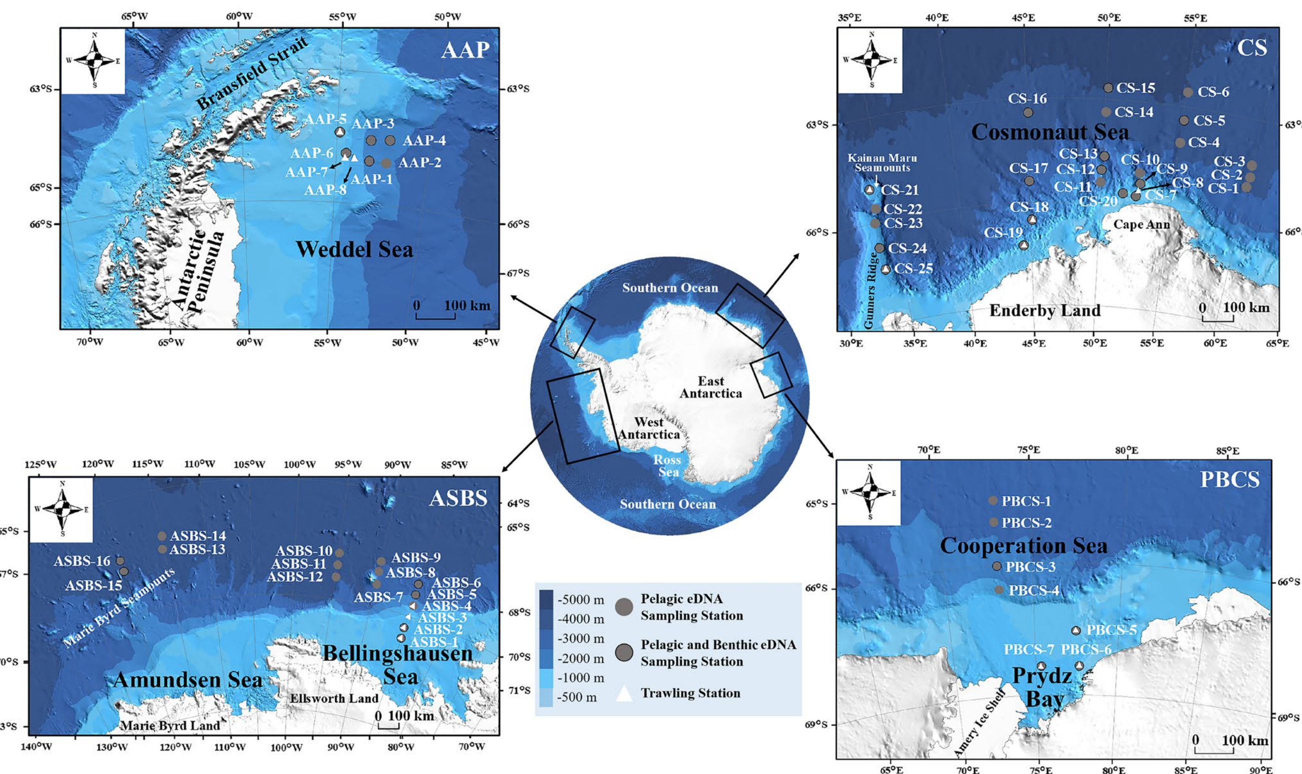

FIGURE 1 | Schematic diagram of bottom trawling and eDNA sampling stations with their relative geographic locations in the Southern Ocean.

was chosen because it provides a favourable platform to study the ecological responses to such changes (Flexas et al. 2022). The ASBS, covered by perennial multiyear ice and home to nearshore polynyas with the highest productivity levels in the Southern Ocean (Arrigo and van Dijken 2003), is one of the least-sampled and most remote high-latitude ice-covered regions for fish studies (Eastman et al. 2013). Meanwhile, it is a known feeding ground for top predators (Riekkola et al. 2019), implying prey resources such as fish may be abundant within the area. However, ASBS is also among the most rapid changing regions in Antarctica, with increasing temperatures and associated significant reductions in extent and duration of sea ice (Mintenbeck et al. 2012). The PBCS, the largest inland incursion in East Antarctica, includes the Amery Ice Shelf and several polynyas. It is a key region for Antarctic Bottom Water formation (Williams et al. 2016) and serves as a typical representative of Antarctic embayment. The CS, characterised by a narrow continental shelf, complex seafloor topography and permanent ice cover, features highly variable sea ice conditions throughout the year. However, the key environmental parameters, such as temperature and sea ice extent, in this region of the Indian Ocean sector of the Southern Ocean remain relatively stable (Chown and Brooks 2019), with little significant impact from climate change observed to date.

2.2 | Trawling and Fish Specimen Collection

To characterise the rough species composition of the fish communities in the study areas and establish a local reference database for taxonomic assignment of ASVs generated from eDNA metabarcoding, three or more hauls were conducted in each area during the CHINARE-37 cruise. Specifically, three bottom trawl stations were conducted in the AAP, four in the ASBS, three in the PBCS, and five in the CS.

All fish specimens were collected using a triangular bottom trawl net (2.2 m wide, 0.65 m high and 6.5 m long; 20 mm mesh size) (Figure S1) deployed from the R/V Xuelong 2 icebreaker during the CHINARE-37 cruise in 2020-2021 (Figure 1 and Table S1). The net was towed at a speed of three knots for 15 min. All captured fish were sorted and provisionally identified to the lowest possible taxonomic level onboard. Their taxonomic identities were later verified in the laboratory using the most up-to-date references (Duhamel et al. 2014; Eastman and Eakin 2021; Gon and Heemstra 1990).

Muscle tissue samples from each fish were preserved in 95% ethanol following the Barcode of Life protocol for fishes to facilitate DNA barcoding analysis (Li et al. 2022) and to establish a local reference database by amplifying MiFish-U primers (Miya et al. 2015). Voucher specimens were counted, weighed and preserved in 95% ethanol at −80°C in the specimen repository of the Third Institute of Oceanography, Ministry of Natural Resources, for long-term preservation.

2.3 | eDNA Sampling, Processing and Data Analyses

A total of 81 water samples were collected from the four regions: AAP (six surface samples and five bottom samples), ASBS (15 surface samples and six bottom samples), PBCS (seven surface samples and four bottom samples), and CS (24 surface samples

1472642, 2025, 7, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ddi.70053 by Kobe University, Wiley Online Library on [23/09/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

and 14 bottom samples) (Figure 1 and Table S2). At each site, 6 L of water was collected either from the surface or 5 m above the bottom using a CTD (Sea-Bird SBE 9/11; Sea-Bird Scientific, Bellevue, WA, USA). Before each sampling, the interiors of the CTD-mounted Niskin were first rinsed with ultrapure water (Milli-Q, 18.2 MΩ cm). Since the Niskin was open before sampling, each was prerinsed with in situ water at each site to minimise cross-contamination between sampling locations. However, due to various constraints during field sampling, only a limited number of bottom seawater samples from each region closely aligned with bottom trawling stations in both location and depth, while the majority exhibited no spatial overlap with trawl sites.

2.3.1 | Water Filtration and DNA Extraction

Following collection, water samples were immediately filtered using 47-mm glass fibre filters (GF/F; GE Healthcare, Buckinghamshire, UK; nominal pore size 0.7 μm). Additionally, 3 L of pure water was filtered as a negative control. After filtration, the filters were stored in a liquid nitrogen tank at −196°C until DNA extraction. To prevent contamination, all equipment used during water collection was decontaminated with a bleach solution (diluted household bleach containing ~0.1% sodium hypochlorite) for over 30 min prior to use to remove residual DNA.

Total eDNA was extracted from the filter samples using the PowerWater DNA Isolation Kit (MoBio Laboratories Inc., Carlsbad, CA, USA; now Qiagen, Hilden, Germany), following the manufacturer's protocol. Each filter was individually placed into a single Salivate tube (Sarstedt, Nümbrecht, Germany) prior to extraction. After extraction, total eDNA was eluted from the DNeasy spin column with 100 μL of Buffer AE (Qiagen). DNA concentration was measured using a NanoDrop ND-1000 Spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA). The extracted DNA samples were stored at −20°C until further eDNA metabarcoding analysis.

2.3.2 | Amplicon Library Preparation and MiSeq Sequencing

Amplicon libraries for fish eDNA metabarcoding were prepared using MiFish-U primers (Miya et al. 2015). The conditions for the first round and second round PCR followed the protocol described by Wu et al. (2021). The second round PCR products from all samples were pooled into a single tube. The library of target-size amplicons was obtained by electrophoresis using the E-Gel SizeSelect 2% system (Thermo Fisher Scientific, Waltham, MA, USA) with the E-Gel Precast Agarose Electrophoresis System (Thermo Fisher Scientific, Waltham, MA, USA).

The isolated DNA was confirmed to be of the target length (approximately 370 bp) using an Agilent 2100 Bioanalyser (Agilent Technologies, Santa Clara, CA, USA). The DNA library concentration was then adjusted to 4 nM. Finally, the library was sequenced using an Illumina MiSeq platform with a v2 Reagent kit for 2 × 250 bp paired-end sequencing (Illumina, San Diego, CA, USA).

2.3.3 | Sequence Data Analysis

The raw reads obtained from MiSeq sequencing were preprocessed and analysed using USEARCH v10.0.240 (Edgar 2010), following the pipeline described in Wu et al. (2021) (see Supporting Information). For ASV alignment and taxonomic annotation, we used a reference database combining sequences from GenBank and a locally curated reference database constructed and validated in our laboratory (Liao et al. 2023). Since many Antarctic fish species lack available 12S rRNA gene sequences, sequences with a similarity of over 98% were accepted and used in the analysis. However, nonfish taxa and fish species distributed outside the Antarctic and sub-Antarctic regions were excluded from further analysis.

2.3.4 | Statistical Analysis

Statistical analyses were conducted using R version 4.3.2 (R Core Team 2024), and the results were visualised accordingly. In all analyses, the sequencing reads data were converted to presence/absence format (Jeunen et al. 2020). For diversity analyses, each sampling region or water layer within each region was treated as the unit of analysis. Analyses started with alpha diversity, then beta diversity, followed by method comparisons and ended up with species accumulation to first resolve ecological patterns, then contextualise methodological performance.

For the trawling results, the R package *circlize* v0.4.15 (Gu et al. 2014) was used to visualise the species composition, individual abundance and proportional representation of fish species in each region. For the eDNA results, a bubble plot was created using the R package *ggplot2* v3.4.4 (Wickham 2011) to present the species composition and relative abundance proportions of fish communities in the surface and bottom layers across the four regions. Boxplots were generated using the R package *vegan* v2.6-4 (Dixon 2003) to calculate and compare the alpha diversity indices (Shannon, Simpson, Chao1 and ACE) of fish communities across the regions, based on both eDNA and trawling data, to assess differences in species richness. Relevant Kruskal-Wallis test was conducted using the R package *stats* 4.3.2 (R Core Team 2024) to examine whether a significant difference existed between the four studied seas. PERMANOVA test based on Bray-Curtis distances was implemented using the R package *vegan* v2.6-4 to compare beta diversity differences among fish communities. Principal coordinates analysis (PCoA) was performed using the R package *phyloseq* v1.46.0 (McMurdie and Holmes 2013) to further visualise the beta diversity differences.

To compare the differences in fish community composition revealed by the two methods (eDNA metabarcoding and trawling) across the four regions, a Venn diagram was created using the R package *VennDiagram* v1.7.3 (Chen and Boutros 2011). Additionally, species accumulation curves were generated to estimate the sampling effort (number of

14724642, 2025, 7, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ddi.70053 by Kobe University, Wiley Online Library on [23/09/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

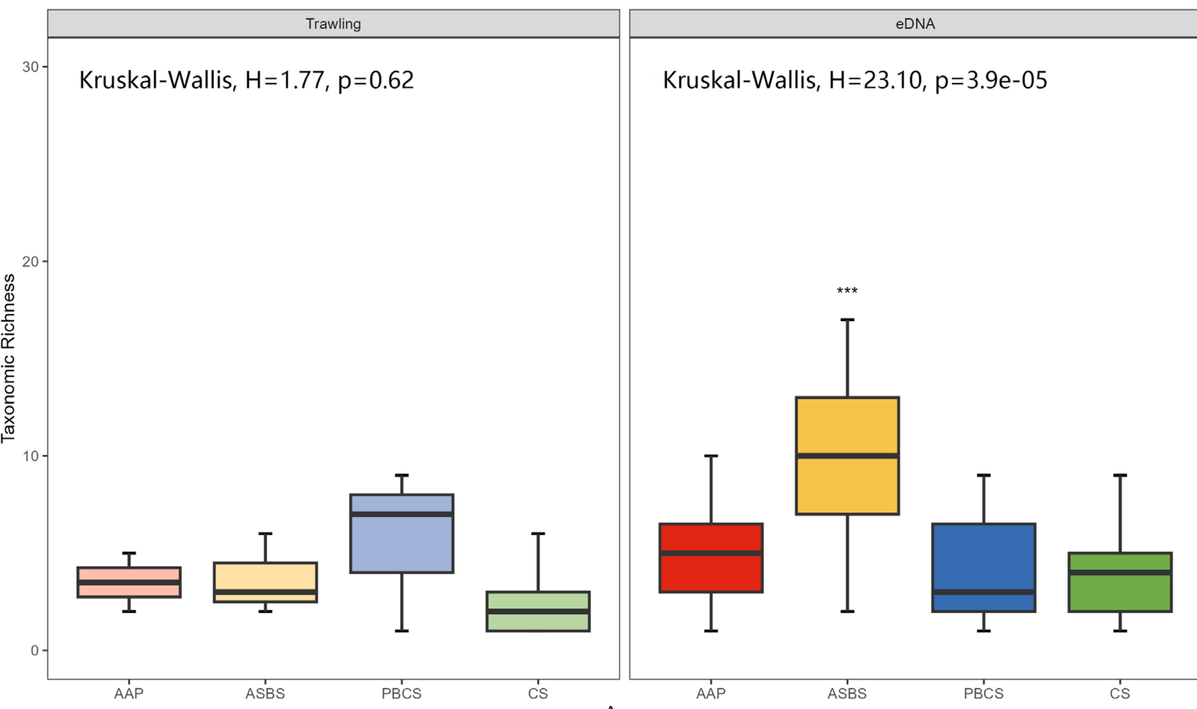

FIGURE 2 | Comparative species richness of area-based fish communities revealed by bottom trawling versus eDNA metabarcoding, with boxplot medians represented by internal lines and H-values and *p* values of the Kruskal–Wallis test annotated above.

trawls or water samples) required to reach species detection saturation. This analysis was conducted using the R package *iNEXT* v3.0.0 (Hsieh et al. 2016). Most of the visualisations, including bubble plots, boxplots and other graphical outputs, were created using the R package *ggplot2* v3.4.4 to ensure clarity and consistency.

To the best of our knowledge, the most recent and authoritative records of Antarctic fish distributions are provided by Duhamel et al. (2014). This book chapter integrates extensive data from various sound and verified sources, making it a highly reliable and authoritative historical dataset on Antarctic fish distributions. The eDNA signals obtained in this study were compared with the distribution records of fish species in the four regions as documented in Duhamel et al. (2014). When necessary, additional references, such as *Fishes of the Southern Ocean* and other literature, were consulted to investigate potential changes in fish distribution ranges or new species records.

3 | Results

3.1 | Fish Catches in Four Studied Antarctic Seas

In the four Antarctic research areas, 101 fish samples were collected during 15 trawling operations. A total of 27 Antarctic fish species, belonging to 23 genera, 6 orders and 10 families, were identified through cross-validation of morphological characteristics and DNA barcoding (Figure S2). In terms of species richness, no significant differences were observed among the regions ($H = 1.77$, $p = 0.62$ in Kruskal-Wallis test; Figure 2). The number of species identified by trawling in each region was as follows: AAP (6 species), ASBS (9 species), PBCS (15 species), and CS (7 species) (Table S1).

3.2 | eDNA Metabarcoding-Based Fish Diversity Analysis

A total of 10,201,946 reads were obtained from the 81 Antarctic eDNA samples. Negative controls processed alongside experimental samples showed no detectable amplification signals, confirming the absence of cross-contamination during laboratory procedures. After bioinformatics filtering, 1,016,035 reads were retained. In total, 40 Antarctic fish species were identified across the four studied areas. Species accumulation curves were also generated to evaluate the sampling effort for eDNA surveys (Figure 3). Overall, *Notothenia coriiceps* dominated or held a significant proportion in fish communities across all water layers in each region. *Macrourus whitsoni* also accounted for a substantial proportion in the surface communities of AAP and CS, as well as in the bottom communities of CS. Other species generally exhibited lower relative abundance or were only dominant in limited water layers and/or seas (Figure 4). In terms of species richness, ASBS showed a highly significant difference compared to the other three regions ($H = 23.10$, $p < 0.001$ in Kruskal-Wallis test; Figure 2). The number of species identified by eDNA in each region was as follows: AAP (18 species), ASBS (30 species), PBCS (15 species), and CS (24 species).

Among the four alpha diversity indices calculated to characterise diversity levels in each region, the Shannon index did not exceed 1.90, and the Simpson index did not exceed 0.85. No significant differences in Shannon and Simpson indices

14724642, 2025, 7, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ddi.70053 by Kobe University, Wiley Online Library on [23/09/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

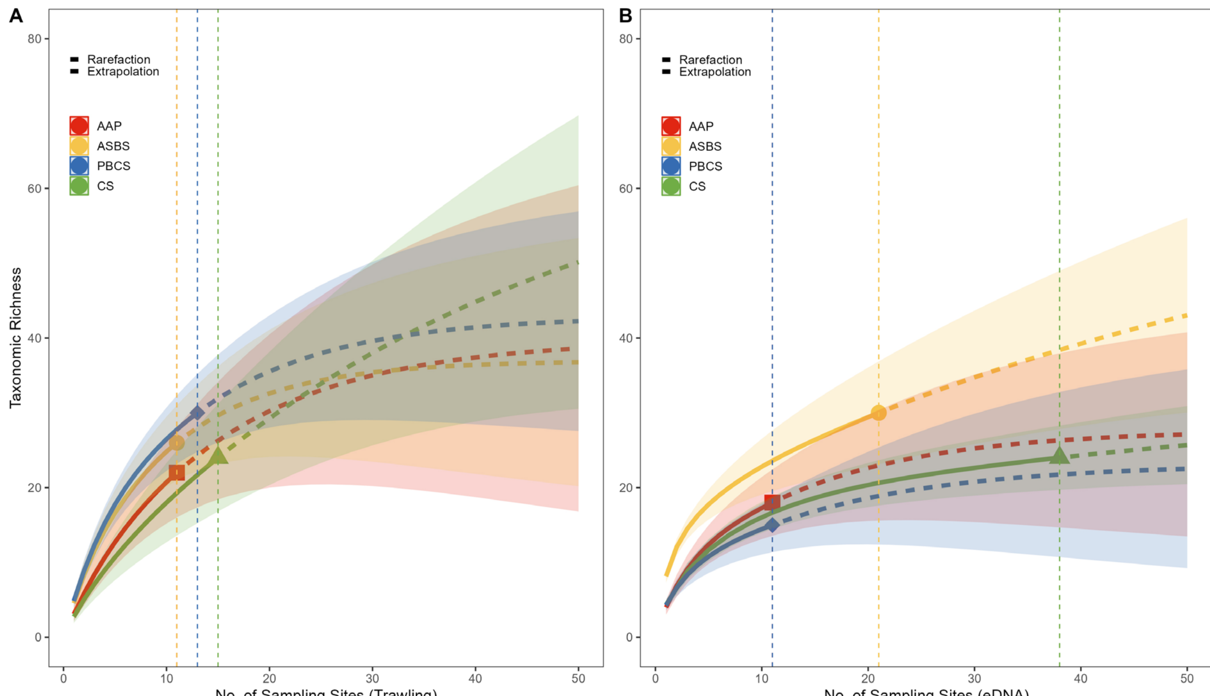

FIGURE 3 | Sampling effort-based species accumulation curves with rarefaction/extrapolation extensions for both eDNA metabarcoding and trawling approaches across study areas.

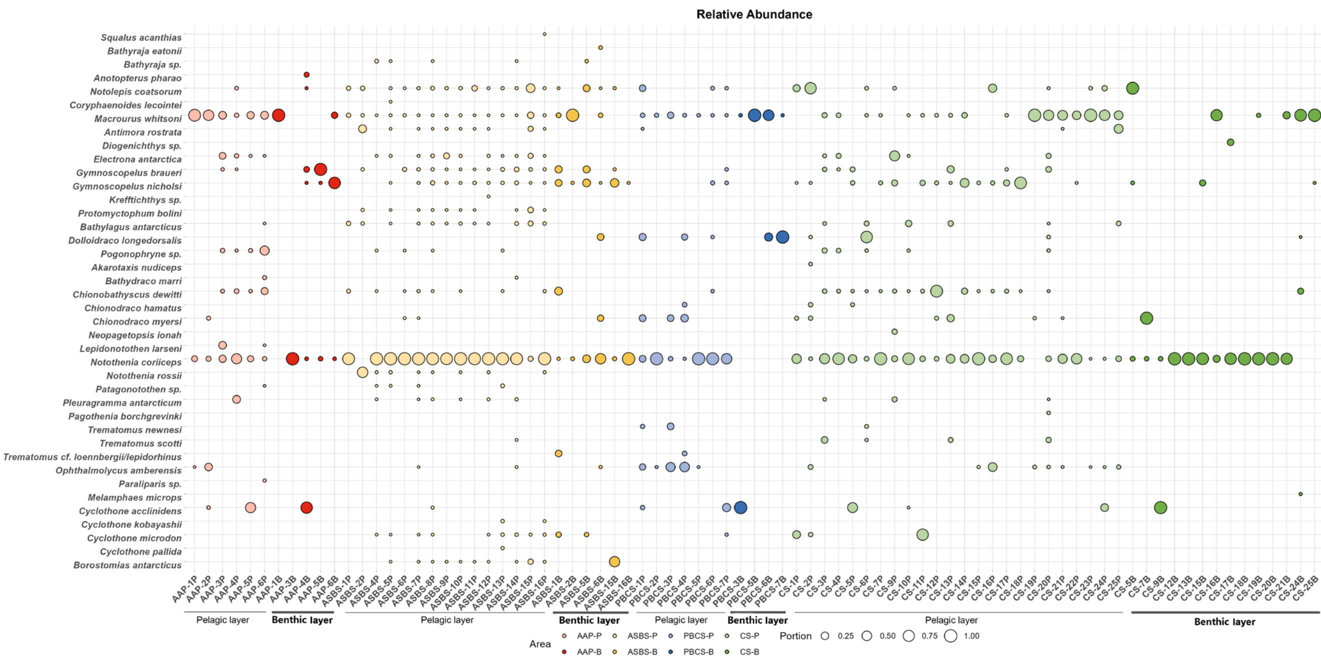

FIGURE 4 | Bubble plot of fish community composition with scaled abundance proportions across depth layers (pelagic vs. benthic) in four studied areas revealed by eDNA metabarcoding. Abbreviations: AAP-P: pelagic fish communities of AAP; AAP-B: benthic fish communities of AAP; ASBS-P: pelagic fish communities of ASBS; ASBS-B: benthic fish communities of ASBS; PBCS-P: pelagic fish communities of PBCS; PBCS-B: benthic fish communities of PBCS; CS-P: pelagic fish communities of CS; CS-B: benthic fish communities of CS.

were observed among the regions. The Chao1 and ACE indices ranged from 3 to 17, with ASBS showing significantly higher Chao1 and ACE indices compared to the other three regions (Figure 5).

For beta diversity, principal coordinates analysis (PCoA) based on Bray-Curtis distances revealed that the surface fish community composition in ASBS differed from the remaining fish communities (Figure 6). The PERMANOVA test based

14724642, 2025, 7, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ddi.70053 by Kobe University, Wiley Online Library on [23/09/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

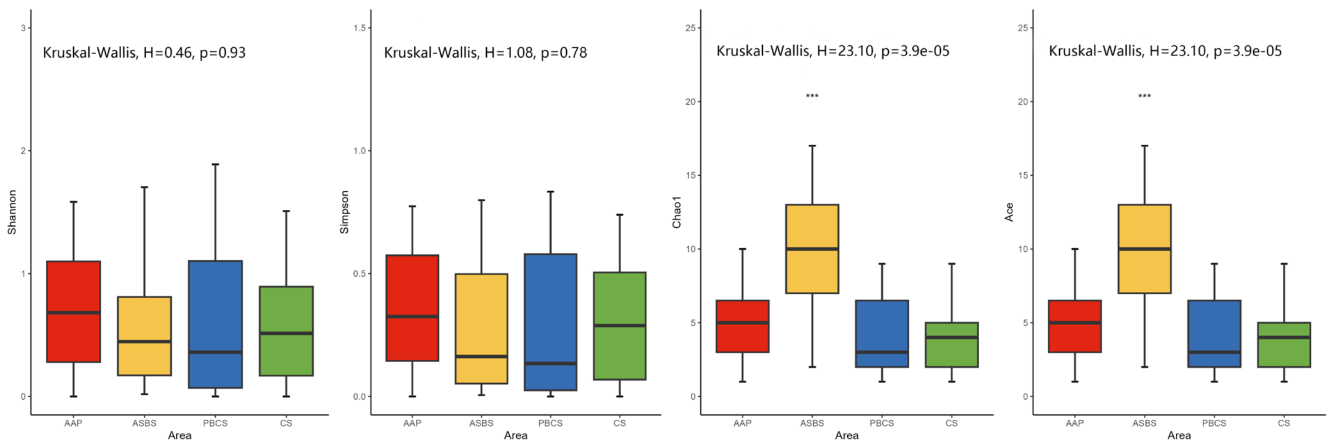

FIGURE 5 | Comparison of α-diversity indices (including Shannon, Simpson, Chao1 and ACE) for fish communities based on eDNA metabarcoding data.

FIGURE 6 | Principal coordinates analysis (PCoA) of vertically partitioned fish assemblages (pelagic layers vs. benthic layers) across four areas based on Bray-Curtis dissimilarity. Abbreviations: AAP-P: pelagic fish communities of AAP; AAP-B: benthic fish communities of AAP; ASBS-P: pelagic fish communities of ASBS; ASBS-B: benthic fish communities of ASBS; PBCS-P: pelagic fish communities of PBCS; PBCS-B: benthic fish communities of PBCS; CS-P: pelagic fish communities of CS; CS-B: benthic fish communities of CS.

14724642, 2025, 7, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ddi.70053 by Kobe University, Wiley Online Library on [23/09/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

on Bray-Curtis distance further verified that the fish community difference existed between ASBS and others ($R^2 = 0.2091$, $p = 0.001$).

3.3 | Comparison Between eDNA Results and Traditional Trawling Surveys and Historical Occurrence Records

A comparison of species detected by eDNA and trawling in each region revealed that both methods identified some overlapping species. However, the proportion of overlapping species relative to the total number of species detected by each method was low (Table S3). Most species were independently identified by one method, with eDNA consistently detecting more species than trawling (Figure S3).

Additionally, species accumulation curves and their extrapolations indicated that, to fully reveal the fish community composition in each region using trawling, a minimum of 11 trawl surveys would be required for AAP and ASBS, 13 surveys for PBCS, and 14 surveys for CS. In contrast, eDNA sampling efforts were closer to reaching asymptotes. However, to achieve optimal results, a minimum of 12 water sampling surveys would be required for AAP and PBCS, 20 surveys for ASBS, and 38 surveys for CS (Figure 3).

Comparative analysis with historical distribution records revealed that 10 of the 40 detected fish species displayed range extensions beyond their previously documented geographical boundaries. Regionally, ASBS exhibited the highest number of expansions (8 cases), followed by the CS (3 cases), AP (2 cases), and PBCS (1 case) (Table 1).

4 | Discussion

4.1 | Performance of eDNA Metabarcoding in Scientific Research and Monitoring of Antarctic Fish Diversity

The effectiveness of eDNA metabarcoding in the study and monitoring of Antarctic fish diversity is a topic of significant interest. To our knowledge, research utilising this method for Antarctic fish studies remains limited, particularly in the oceanic regions of the Southern Ocean. Among the few studies available, Liao et al. (2023) provided a comparative evaluation of the effectiveness of eDNA metabarcoding and an established fishing method in assessing fish diversity. While their study preliminarily validated the effectiveness of eDNA metabarcoding in the Southern Ocean, the research was limited to the CS region, a marginal sea and thus had a relatively narrow spatial scale. In contrast, this study adopts a circumpolar approach, collecting eDNA samples and conducting trawling operations simultaneously across multiple regions, allowing for a more comprehensive evaluation of the performance of eDNA metabarcoding in the Southern Ocean.

Comparatively, the sampling sites required for eDNA to identify the whole fish community composition in each region

TABLE 1 | Comparison of fish species signals detected by eDNA and corresponding historical distribution records across Antarctic seas.

Species name	AAP	ASBS	PBCS	CS
Squalus acanthias	—	?	—	—
Bathyraja eatonii	—	✓	—	—
Bathyraja sp.	—	✓	—	—
Notolepis coatsorum	✓	✓	✓	✓
Anotopterus pharao	✓	—	—	—
Coryphaenoides lecointei	—	✓	—	—
Macrourus whitsoni	✓	✓	✓	✓
Antimora rostrata	—	✓	✓	✓
Diogenichthys sp.	—	—	—	?
Electrona antarctica	✓	✓	—	✓
Gymnoscopelus braueri	✓	✓	✓	✓
Gymnoscopelus nicholsi	✓	✓	✓	✓
Krefftichthys sp.	—	✓	—	—
Protomyctophum bolini	—	✓	—	—
Bathylagus antarcticus	✓	✓	—	✓
Dolloidraco longedorsalis	✓	?	✓	✓
Pogonophryne sp.	✓	✓	✓	—
Akarotaxis nudiceps	—	—	—	✓
Bathydraco marri	✓	?	—	—
Chionobathyscus dewitti	✓	✓	✓	✓
Chionodraco hamatus	—	—	✓	✓
Chionodraco myersi	✓	✓	✓	✓
Neopagetopsis ionah	—	—	✓	—
Lepidonotothen larseni	✓	—	—	—
Notothenia coriiceps	✓	✓	✓	✓
Notothenia rossii	—	?	—	—
Patagonotothen sp.	?	?	—	—
Pleuragramma antarcticum	✓	✓	✓	✓

(Continues)

14724642, 2025, 7, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ddi.70053 by Kobe University, Wiley Online Library on [23/09/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 1 | (Continued)

Species name	AAP	ASBS	PBCS	CS
Pagothenia borchgrevinki	—	—	✓	—
Trematomus newnesi	—	✓	✓	—
Trematomus scotti	—	✓	—	✓
Trematomus cf. *loennbergii/lepidorhinus*	—	✓	—	—
Ophthalmolycus amberensis	✓	✓	✓	✓
Paraliparis sp.	—	✓	—	—
Melamphaes microps	—	—	—	
Cyclothone acclinidens	?	?	?	?
Cyclothone kobayashii	—	✓	✓	—
Cyclothone microdon	—	✓	✓	?
Cyclothone pallida	—	?	—	—
Borostomias antarcticus	—	?	—	—

Note: "✓" indicates that the detected species distribution matches historical records; "?" denotes a discrepancy between detected and historical distributions; "-" signifies no signal of the species detected in the respective sea area.

are generally slightly higher than those required for trawling except for ASBS (Figure 3). However, eDNA sampling offers clear advantages over traditional methods such as trawling in terms of convenience, time, labour costs and research efficiency (Yao et al. 2022). In each region, some fish species were detected by both eDNA metabarcoding and bottom trawling. Although eDNA metabarcoding occasionally missed some species captured by trawling, it consistently identified a greater number of species that were not captured by trawling. This result can be attributed to several factors: (1) the depth of bottom water samples collected for eDNA analysis did not always correspond well with the depths targeted by bottom trawling, and Antarctic fish species often exhibit vertical distribution patterns restricted to specific depths (Eastman 2017); (2) inherent biases in metabarcoding primers and the PCR process may have prevented the effective detection of some low-abundance species (Takeuchi et al. 2019); (3) the quality of the reference database plays a critical role in determining the extent to which local species information can be recovered. In fact, many ASVs in this study were annotated at the species level only with the support of our curated reference database (Liao et al. 2023), including species such as *Bathylagus antarcticus*, *Bathydraco marri*, *Chionodraco hamatus* and *Lepidonotothen larseni*. However, some species were annotated only at the genus level due to the absence of relevant sequences in public databases or limitations in our curated database. For example, *Krefftichthys* sp., despite being monotypic (Duhamel et al. 2014), could only be annotated at the genus level due to the lack of reference sequences. This raises the possibility that some species were filtered out due to incomplete annotation information.

It is also worth noting that the results of this study, which simultaneously employed eDNA metabarcoding and trawling to assess Antarctic fish diversity in the Southern Ocean, are broadly consistent with but differ in certain aspects from those of Liao et al. (2023). In their study, the proportion of species detected by both methods was higher, while the proportion of species uniquely detected by each method was lower. Several factors may explain these differences: First, Liao et al. (2023) utilised both 12S rRNA and 16S rRNA gene markers, which effectively increased the detection probability of rare species and species with poor primer specificity, thereby improving their coverage of species captured by bottom trawling compared to this study, which used only a single molecular marker. Second, this study did not include sediment as an additional eDNA source, which could have better captured species detected by bottom trawling. Third, and most importantly, unlike Liao et al. (2023), where eDNA sampling sites largely overlapped with trawling sites, this study faced significant environmental constraints, including water depth, topography, substrate type, weather conditions and sea ice coverage. As a result, only a small portion of trawling sites overlapped with eDNA sampling sites, and these were mostly located on the continental shelf and upper slope (Table S1). In contrast, eDNA sampling sites were more frequently positioned in deep offshore regions (Table S2). Consequently, differences in sampling site setups between the two methods were reflected in the composition of fish species detected. In terms of species richness, pelagic midwater and upper-layer fish species, or cartilaginous fishes such as *Bathyraja eatonii* and *Squalus acanthias*, which are difficult to capture with bottom trawling (Li et al. 2024), were more prominent among species detected by eDNA. Meanwhile, species typically representing nearshore shelf and upper slope fish communities dominated the trawling catches. Species detected by both methods were generally common species with high local abundance, such as *B. marri* and *M. whitsoni* in AAP (see Table S1 and other unpublished data), *Chionobathyscus dewitti* and *M. whitsoni* in the ASBS (Eastman et al. 2013), *Dolloidraco longedorsalis* and *Chionodraco myersi* in PBCS (Li et al. 2022) and *M. whitsoni*, *Trematomus* cf. *loennbergii/lepidorhinus* (Li et al. 2024) and *E. antarctica* (Van de Putte et al. 2010) in CS. These findings further confirm the effectiveness of eDNA metabarcoding in fish research and monitoring on a circumpolar scale in the Southern Ocean, highlighting its role as a valuable complement to traditional methods such as bottom trawling.

4.2 | eDNA Metabarcoding Demonstrated Its Potential for Monitoring Antarctic Ichthyoplankton

In this study, eDNA metabarcoding also demonstrated potential for application in the research and monitoring of Antarctic fish planktonic stages. The early life stages of most Southern Ocean fish species remain poorly described, largely due to the lack of surveys in many regions, benthic egg-laying habits (e.g., eggs

14724642, 2025, 7, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ddi.70053 by Kobe University, Wiley Online Library on [23/09/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

attached to sponges) and the logistical challenges of winter sampling (Koubbi et al. 2009). Environmental DNA technology has already been shown to sensitively and accurately detect spawning and larval migration activities in fish (Wu et al. 2019; Wu et al. 2023), suggesting that it could provide solutions to these challenges. In this study, the distribution signals of several species detected are more likely to reflect the activity of larvae rather than adults. For instance, *N. coriiceps* and *N. rossii* are widely distributed Antarctic fishes that typically spawn in austral autumn, with hatching periods exceeding 3 months. Posthatching larvae have a pelagic phase lasting at least 6-8 months, during which they exhibit near-neutral buoyancy before eventually settling in habitats as deep as 550 m (Eastman 2017; Eastman et al. 2011). Given that all ASBS sampling sites in this study were deeper than 550 m, it is unlikely that the eDNA signals of *N. coriiceps* detected in deep waters originated from adults. Similarly, as this species is a sedentary demersal fish (North 1996), its eDNA signals in pelagic waters are also unlikely to originate from adults. Sampling in the ASBS region occurred in early 2021, coinciding with the pelagic larval phase of *N. coriiceps* characterised by neutral buoyancy. Interestingly, the Argentine Islands near the Bellingshausen Sea were considered potential spawning or nursery grounds for *N. coriiceps* and *N. rossii* (Trokhymets et al. 2022), and eggs released during spawning and subsequent larval development are theoretically transported by the Antarctic Coastal Current to the ASBS sampling sites in this study. Although the *N. rossii* signals detected in ASBS pelagic waters cannot be directly attributed to larval stages like those of *N. coriiceps*, their presence can be indirectly linked to larval transport by the Antarctic Coastal Current, given the high degree of life history similarity between the two species. Additionally, the historical overfishing of *N. rossii*, which led to significant population declines, and the absence of commercial fishing for *N. coriiceps* (Kock 1992), are reflected in the relative abundance ratios of the two species at ASBS sampling sites. Collectively, these findings strongly suggest that the eDNA signals of *N. coriiceps* and *N. rossii* detected in ASBS likely originated from their pelagic larval stages, demonstrating the potential of eDNA metabarcoding for studying and monitoring the early life stages of Antarctic fishes.

4.3 | Fish Diversity Patterns in the Four Studied Antarctic Seas

The diversity levels characterised by the alpha diversity indices across the four studied seas were consistent with findings from previous studies (Liao et al. 2023). Although the Shannon and Simpson indices of the fish community in AAP were higher than those in the other three regions, the differences were not statistically significant. This result aligns, on one hand, with the general pattern that fish diversity tends to be higher in lower-latitude regions such as AAP. On the other hand, it also suggests that the influence of such differences is overshadowed by the overall homogenising effects of the extreme Antarctic environment in shaping local fish communities. Meanwhile, we observed that both the Chao1 and ACE indices in ASBS were significantly higher than those in the other three seas, reflecting a higher species richness detected in this region. Considering that the number of eDNA samples collected in ASBS was not significantly greater than in other regions and that the species accumulation curve did not reach an asymptote, this suggested that the species richness in ASBS, as a potential biodiversity hotspot, may have been underestimated and deserve more conservation effort. And given that ASBS remains an understudied area in Antarctic fish research (Eastman et al. 2013; Trokhymets et al. 2022), further sampling efforts and long-term monitoring in this region are strongly encouraged.

In this study, we detected eDNA signals for 40 Antarctic fish species using the MiFish universal primers. These species included common Notothenioidei groups such as Artedidraconidae, Bathydraconidae, Channichthyidae and Nototheniidae, as well as other common non-Notothenioidei groups, including Rajidae, Paralepididae, Macrouridae, Myctophidae, Bathylagidae, Zoarcidae and Liparidae. Additionally, the dataset encompassed several relatively rare groups with known distributions in Antarctic waters, such as Squalidae, Moridae, Melamphaidae, Gonostomatidae and Stomiidae. Overall, the fish community composition revealed by eDNA metabarcoding aligns with the general patterns reported in previous studies, which indicate that Notothenioidei dominate the Antarctic fish fauna while other typical deep-sea taxa are also present (Duhamel et al. 2014; Mintenbeck et al. 2012). However, it is worth noting that the dominance of Notothenioidei in this study was primarily driven by the high relative abundance of *N. coriiceps* eDNA sequences in most samples. In terms of species richness, typical deep-sea taxa had a greater number of species, which contrasts with the fish community composition typical of nearshore shelf and upper slope regions in Antarctica (Eastman 2005). This is likely due to the fact that the eDNA sampling stations in this study were predominantly located in deep-sea regions beyond the continental shelf.

Additionally, we observed that some benthic fish species appeared in pelagic fish communities, while certain pelagic and mesopelagic fish species were also detected in bottom water samples. We propose several possible explanations for this phenomenon: first, many pelagic and mesopelagic fish (Van de Putte et al. 2010), certain benthic fish (Mintenbeck et al. 2012) and their respective predators (Hanchet et al. 2015) exhibit vertical movement behaviours, releasing eDNA into both bottom and pelagic water layers during their movements. Second, free eDNA particles released by pelagic and mesopelagic fish often sink to deeper water layers due to their size and gravity, while eDNA from benthic fish may be transported to upper water layers through upwelling and particle resuspension (Jeunen et al. 2020). Finally, the early life stages of some benthic fish species are planktonic (Calì et al. 2017; Duhamel et al. 2014; Koubbi et al. 2009) and release eDNA into the water column.

The beta diversity results revealed differences in fish communities among the studied seas. Contrary to our initial hypothesis that fish communities in the West Antarctic seas (AAP and ASBS) would differ significantly from those in the East Antarctic seas (CS and PBCS), the eDNA results showed that the only significant difference in community structure was between the surface fish community in ASBS and the bottom fish community in ASBS, as well as the surface and bottom fish communities in the other three regions. This difference was primarily driven by the significant dominance of *N. coriiceps* in the surface fish community of ASBS rather than impacts of climate change, which can be attributed to the large number of *N.*

14724642, 2025, 7, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ddi.70053 by Kobe University, Wiley Online Library on [23/09/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

coriiceps individuals in their early planktonic life stages in this region, as previously discussed.

4.4 | Potential Drivers of Species Distribution Shifts Beyond Historical Records

The primary objective of comparing eDNA signals with historical records of Antarctic fish distributions in this study was to understand the fish diversity patterns in Antarctic seas affected by climate change and, in particular, to determine whether species distributions have extended beyond previously recorded ranges. Our analysis revealed that, of the 40 Antarctic fish species detected via eDNA, 10 species exhibited distribution ranges that extended beyond historical records. Among these, *B. marri*, *D. longedorsalis*, *Cyclothone kobayashii* and *C. microdon* are circum-Antarctic species that were detected in ASBS and/or CS. Their presence in these regions is likely due to insufficient prior surveys, which have limited our understanding of ecological baselines. Similarly, *Borostomias antarcticus* and *C. acclinidens* are typical deep-sea mesopelagic fish species primarily distributed in sub-Antarctic waters (Duhamel et al. 2014). However, their presence in ASBS and across all four regions, respectively, can be reasonably attributed to new records resulting from previously inadequate surveys, as *B. antarcticus* has been recorded in the Ross Sea (Hanchet et al. 2013) and *C. acclinidens* in the Lazarev Sea (Gon and Heemstra 1990). The new record of *N. rossii* in ASBS has already been discussed, as it is likely related to its planktonic early life stages. *Diogenichthys* sp. is represented in the Southern Ocean by a single species, *Diogenichthys atlanticus*, which has been recorded occasionally south of the Subtropical Front (Duhamel et al. 2014). Given this, its presence in CS is plausible. Similarly, the widely distributed *S. acanthias* occasionally migrates to the waters around the Kerguelen Islands (Duhamel et al. 2014). Its detection in ASBS, near the Marie Byrd Seamounts, is likely a snapshot of its foraging activity, as seamounts are typically regions of high productivity with abundant food resources (Sergi et al. 2020).

Among all the new records, *Patagonotothen* sp. warrants special attention. The absence of *Patagonotothen* sequences in negative controls, combined with strict field and laboratory protocols, eliminates exogenous DNA contamination risks. Notably, (1) our laboratory has no historical capture records of *Patagonotothen* spp. in Antarctic waters, and (2) the R/V Xuelong 2 had never operated within this genus's traditional distribution range prior to this study. These safeguards confirm the validity of the *Patagonotothen* sp. environmental DNA signals detected in AAP and ASBS. It is generally believed that the only species of this genus with a trans-Antarctic Polar Front range is *Patagonotothen guntheri*, which extends from the southern Patagonian Shelf to the Shag Rocks Shelf (Ceballos et al. 2019) (Figure S4). Therefore, regardless of the specific species of *Patagonotothen* sp. detected in AAP and ASBS, its activity has clearly exceeded the previously recorded southernmost distribution limit.

Marine fish with dispersal capabilities typically respond to climate warming through changes in abundance, habitat depth and geographic distribution (Perry et al. 2005; Simpson et al. 2011). Such changes are particularly pronounced in high-latitude regions due to rapid temperature increases and persistent sea ice retreat in polar ecosystems (Hollowed et al. 2013). For example, in the Arctic, some fish species are gradually shifting their habitats poleward (Zhang et al. 2022). In the Antarctic, although warming and sea ice retreat have also been observed in West Antarctica (Convey and Peck 2019; Rignot et al. 2013), no reports of fish range shifts or poleward expansions have been documented to date. For Antarctic Notothenioidei species, their stenothermy and lack of alternative habitats at the highest latitudes limit their capacity for large-scale poleward expansion (Mintenbeck et al. 2012). However, for Notothenioidei species inhabiting sub-Antarctic islands, particularly *Patagonotothen* spp., which are believed to have originated in Antarctic waters (Ceballos et al. 2019), poleward expansion into the increasingly warm AAP via stepping stones such as the Scotia Arc (Mintenbeck et al. 2012) and mesoscale eddies (Chown et al. 2015) is not inconceivable. Nevertheless, as with other species detected solely through eDNA, the distribution signal of *Patagonotothen* sp. in AAP and ASBS should be treated cautiously and requires further confirmation through net-based surveys or in situ imaging. Regardless, the observed changes in fish diversity patterns in climate-sensitive regions such as AAP and ASBS warrant special attention, as they may indicate long-term shifts in Antarctic marine ecosystems in both the Western and Eastern Antarctic seas.

5 | Conclusions

Based on the CHINARE-37 cruise, we conducted the first circumpolar scale study of the Antarctic fish diversity using eDNA metabarcoding. Our results demonstrated that: (1) eDNA metabarcoding may exhibit potential for tracking early life stages of Antarctic fishes and could effectively complement traditional surveys. (2) Fish diversity in the four studied areas generally aligns with the general patterns of the Southern Ocean as previously revealed by others, but the ASBS may represent a fish diversity hotspot. (3) Despite requiring further confirmation via fishing gears or in situ imaging, the detection of *Patagonotothen* sp. beyond its historically documented southern range boundary suggests potential climate-driven redistribution and signals future trajectories for Antarctic marine ecosystems.

Moving forward, it is essential to integrate eDNA metabarcoding into the research and monitoring of Antarctic fish. This can be achieved by constructing high-quality local reference databases, collecting eDNA from various sources, employing multiple molecular markers and optimising sampling strategies and data analysis workflows, thereby providing an effective complement to traditional techniques such as trawling (Liao et al. 2023). Ultimately, the combined use of fishing gears, in situ imaging and eDNA metabarcoding will enable comprehensive surveys of fish ecological baselines in remote or data-deficient regions of the Southern Ocean, track spatiotemporal changes in Antarctic fish diversity patterns across multiple scales and enhance our understanding of the dynamic impacts of climate change on Antarctic marine ecosystems.

Author Contributions

Hai Li: conceptualization, data collection, data curation, formal analysis, funding acquisition, methodology, writing – original draft

14724642, 2025, 7, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ddi.70053 by Kobe University, Wiley Online Library on [23/09/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

preparation, writing-review and editing. **Fang Yang:** conceptualization, formal analysis, methodology, writing-original draft preparation. **Yuzhuo Liao:** data collection, data curation, formal analysis, methodology, visualization. **Xiang Zhang:** formal analysis, methodology, visualization. **Yuan Li:** conceptualization, funding acquisition, project administration, resources. **Rui Wang:** funding acquisition, project administration, resources. **Ran Zhang:** methodology, visualization. **Dong Li:** methodology. **Qianqian Wu:** conceptualization, data collection, data curation, methodology, resources, writing-original draft preparation, writing-review and editing. **Longshan Lin:** funding acquisition, project administration, resources, writing-review and editing.

Acknowledgements

This work was supported by the National Key Research and Development Program of China (2023YFF0611803); the Scientific Research Foundation (2025036) and the 'Cultivating Innovation Team' Program of the Third Institute of Oceanography, Ministry of Natural Resources and the 'Impact and Response of Antarctic Seas to Climate Change' program (IRASCC01-02-02, IRASCC02-02), Chinese Arctic and Antarctic Administration. We extend our gratitude to the crew and scientific team of R/V Xuelong 2 for their exceptional support during the CHINARE-37. Special acknowledgements are due to Chief Scientist Dr. Jun Zhao for his exemplary leadership in navigating the operational challenges posed by the COVID-19 pandemic, and Mr. Wensheng Lin for his expertise and efforts in coordinating demersal trawling operations and eDNA sampling.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The raw sequencing data generated in this study have been deposited in the NCBI Sequence Read Archive (SRA) under the Bioproject accession number SPR32673577-SPR32673502. Processed ASV tables and metadata are available in the Supporting Information.

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.70053.

References

Armour, K. C., J. Marshall, J. R. Scott, A. Donohoe, and E. R. Newsom. 2016. "Southern Ocean Warming Delayed by Circumpolar Upwelling and Equatorward Transport." *Nature Geoscience* 9, no. 7: 549–554. https://doi.org/10.1038/NGEO2731.

Arrigo, K. R., and G. L. van Dijken. 2003. "Phytoplankton Dynamics Within 37 Antarctic Coastal Polynya Systems." *Journal of Geophysical Research* 108: 219–227. https://doi.org/10.1029/2002JC001739.

Atkinson, A., S. L. Hill, E. A. Pakhomov, et al. 2019. "Krill (*Euphausia superba*) Distribution Contracts Southward During Rapid Regional Warming." *Nature Climate Change* 9: 142–147. https://doi.org/10.1038/s41558-018-0370-z.

Calì, F., E. Riginella, M. La Mesa, and C. Mazzoldi. 2017. "Life History Traits of *Notothenia Rossii* and *N. coriiceps* Along the Southern Scotia Arc." *Polar Biology* 40: 1409–1423. https://doi.org/10.1007/s00300-016-2066-z.

Ceballos, S. G., M. Roesti, M. Matschiner, et al. 2019. "Phylogenomics of an Extra-Antarctic Notothenioid Radiation Reveals a Previously Unrecognized Lineage and Diffuse Species Boundaries." *BMC Ecology and Evolution* 19, no. 13. https://doi.org/10.1186/s12862-019-1345-z.

Chen, H., and P. C. Boutros. 2011. "*VennDiagram*: A Package for the Generation of Highly-Customizable Venn and Euler Diagrams in R." *BMC Bioinformatics* 12: 35. https://doi.org/10.1186/1471-2105-12-35.

Chown, S. L., and C. M. Brooks. 2019. "The State and Future of Antarctic Environments in a Global Context." *Annual Review of Environment and Resources* 44: 1–30. https://doi.org/10.1146/annurev-environ-101718-033236.

Chown, S. L., A. Clarke, C. I. Fraser, S. C. Cary, K. L. Moon, and M. A. McGeoch. 2015. "The Changing Form of Antarctic Biodiversity." *Nature* 522: 431–438. https://doi.org/10.1038/nature14505.

Christiansen, H., A. Dettai, F. M. Heindler, et al. 2018. "Diversity of Mesopelagic Fishes in the Southern Ocean – a Phylogeographic Perspective Using DNA Barcoding." *Frontiers in Ecology and Evolution* 6: 120. https://doi.org/10.3389/fevo.2018.00120.

Comiso, J. C., R. A. Gersten, L. V. Stock, J. Turner, G. J. Perez, and K. Cho. 2017. "Positive Trend in the Antarctic Sea Ice Cover and Associated Changes in Surface Temperature." *Journal of Climate* 30, no. 6: 2251–2267. https://doi.org/10.1175/jcli-d-16-0408.1.

Constable, A. J., J. Melbourne Thomas, S. P. Corney, et al. 2014. "Climate Change and Southern Ocean Ecosystems I: How Changes in Physical Habitats Directly Affect Marine Biota." *Global Change Biology* 20, no. 10: 3004–3025. https://doi.org/10.1111/gcb.12623.

Convey, P., and L. S. Peck. 2019. "Antarctic Environmental Change and Biological Responses." *Science Advances* 5, no. 11: eaaz0888. https://doi.org/10.1126/sciadv.aaz0888.

Dixon, P. 2003. "*VEGAN*, a Package of R Functions for Community Ecology." *Journal of Vegetation Science* 14, no. 6: 927–930. https://doi.org/10.1111/j.1654-1103.2003.tb02228.x.

Djurhuus, A., C. J. Closek, R. P. Kelly, et al. 2020. "Environmental DNA Reveals Seasonal Shifts and Potential Interactions in a Marine Community." *Nature Communications* 11, no. 254. https://doi.org/10.1038/s41467-019-14105-1.

Duhamel, G., M. Belchier, P. A. Hulley, et al. 2014. "Biogeographic Patterns of Fish." In *Biogeographic Atlas of the Southern Ocean*. Scientific Committee on Antarctic Research. https://doi.org/10.13140/2.1.1828.3203.

Eastman, J. T. 1993. *Antarctic Fish Biology: Evolution in a Unique Environment*. Academic Press.

Eastman, J. T. 2005. "The Nature of the Diversity of Antarctic Fishes." *Polar Biology* 28: 93–107. https://doi.org/10.1007/s00300-004-0667-4.

Eastman, J. T. 2017. "Bathymetric Distributions of Notothenioid Fishes." *Polar Biology* 40: 2077–2095. https://doi.org/10.1007/s00300-017-2128-x.

Eastman, J. T., M. O. Amsler, R. B. Aronson, et al. 2013. "Photographic Survey of Benthos Provides Insights Into the Antarctic Fish Fauna From the Marguerite Bay Slope and the Amundsen Sea." *Antarctic Science* 25, no. 1: 31–43. https://doi.org/10.1017/S0954102012000697.

Eastman, J. T., E. Barrera-Oro, and E. Moreira. 2011. "Adaptive Radiation at a Low Taxonomic Level: Divergence in Buoyancy of the Ecologically Similar Antarctic Fish *Notothenia Coriiceps* and *N. Rossii*." *Marine Ecology Progress Series* 438: 195–206. https://doi.org/10.3354/meps09287.

Eastman, J. T., and R. R. Eakin. 2021. "Checklist of the Species of Notothenioid Fishes." *Antarctic Science* 33, no. 3: 273–280. https://doi.org/10.1017/S0954102020000632.

Edgar, R. 2010. "Usearch: Lawrence Berkeley National Lab (LBNL)".

Flexas, M. M., A. F. Thompson, M. P. Schodlok, H. Zhang, and K. Speer. 2022. "Antarctic Peninsula Warming Triggers Enhanced Basal Melt Rates Throughout West Antarctica." *Science Advances* 8, no. 32: eabj9134. https://doi.org/10.1126/sciadv.abj9134.

Fogarty, H. E., M. T. Burrows, G. T. Pecl, L. M. Robinson, and E. S. Poloczanska. 2017. "Are Fish Outside Their Usual Ranges Early Indicators of Climate-Driven Range Shifts?" *Global Change Biology* 23, no. 5: 2047–2057. https://doi.org/10.1111/gcb.13635.

14724642, 2025, 7, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ddi.70053 by Kobe University, Wiley Online Library on [23/09/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Gon, O., and P. C. Heemstra. 1990. *Fishes of the Southern Ocean*. JLB Smith Institute of Ichthyology.

Griffiths, H. J. 2010. "Antarctic Marine Biodiversity–What Do We Know About the Distribution of Life in the Southern Ocean?" *PLoS One* 5, no. 8: e11683. https://doi.org/10.1371/journal.pone.0011683.

Griffiths, H. J., R. J. Whittle, S. J. Roberts, et al. 2013. "Antarctic Crabs: Invasion or Endurance?" *PLoS One* 8, no. 7: e66981. https://doi.org/10.1371/journal.pone.0066981.

Gu, Z., L. Gu, R. Eils, M. Schlesner, and B. Brors. 2014. ""Circlize" Implements and Enhances Circular Visualization in R." *Bioinformatics* 30, no. 19: 2811–2812. https://doi.org/10.1093/bioinformatics/btu393.

Gutt, J., E. Isla, J. C. Xavier, et al. 2021. "Antarctic Ecosystems in Transition-Life Between Stresses and Opportunities." *Biological Reviews* 96, no. 3: 798–821. https://doi.org/10.1111/brv.12679.

Hanchet, S., A. Dunn, S. Parker, P. Horn, D. Stevens, and S. Mormede. 2015. "Antarctic Toothfish (*Dissostichus mawsoni*): Biology, Ecology, and Life History in the Ross Sea Region." *Hydrobiologia* 761: 397–414. https://doi.org/10.1007/s10750-015-2435-6.

Hanchet, S. M., A. L. Stewart, P. J. McMillan, M. R. Clark, R. L. O'Driscoll, and M. L. Stevenson. 2013. "Diversity, Relative Abundance, New Locality Records, and Updated Fish Fauna of the Ross Sea Region." *Antarctic Science* 25, no. 5: 619–636. https://doi.org/10.1017/S0954102012001265.

Haumann, F. A., N. Gruber, M. Munnich, I. Frenger, and S. Kern. 2016. "Sea-Ice Transport Driving Southern Ocean Salinity and Its Recent Trends." *Nature* 537: 89–92. https://doi.org/10.1038/nature19101.

Hollowed, A. B., B. Planque, and H. Loeng. 2013. "Potential Movement of Fish and Shellfish Stocks From the Sub-Arctic to the Arctic Ocean." *Fisheries Oceanography* 22, no. 5: 355–370. https://doi.org/10.1111/fog.12027.

Howell, L., M. LaRue, and S. P. Flanagan. 2021. "Environmental DNA as a Tool for Monitoring Antarctic Vertebrates." *New Zealand Journal of Zoology* 48, no. 3–4: 245–262. https://doi.org/10.1080/03014223.2021.1900299.

Hsieh, T. C., K. H. Ma, and A. Chao. 2016. "iNEXT: An R Package for Rarefaction and Extrapolation of Species Diversity (Hill Numbers)." *Methods in Ecology and Evolution* 7, no. 12: 1451–1456. https://doi.org/10.1111/2041-210X.12613.

Hughes, K. A., O. L. Pescott, J. Peyton, et al. 2020. "Invasive Non-Native Species Likely to Threaten Biodiversity and Ecosystems in the Antarctic Peninsula Region." *Global Change Biology* 26, no. 4: 2702–2716. https://doi.org/10.1111/gcb.14938.

Jeunen, G. J., M. D. Lamare, M. Knapp, et al. 2020. "Water Stratification in the Marine Biome Restricts Vertical Environmental DNA (eDNA) Signal Dispersal." *Environmental DNA* 2, no. 1: 99–111. https://doi.org/10.1002/edn3.49.

Kock, K. H. 1992. *Antarctic Fish and Fisheries*. Cambridge University Press.

Koubbi, P., G. Duhamel, J. Hecq, et al. 2009. "Ichthyoplankton in the Neritic and Coastal Zone of Antarctica and Subantarctic Islands: A Review." *Journal of Marine Systems* 78, no. 4: 547–556. https://doi.org/10.1016/j.jmarsys.2008.12.024.

La Mesa, M., G. Mesa, D. Piepenburg, J. Gutt, and J. T. Eastman. 2022. "Spatial Patterns and Behaviour of Notothenioid Fishes Off the Northern Antarctic Peninsula." *Polar Biology* 45: 971–985. https://doi.org/10.1007/s00300-022-03047-y.

Li, H., S. Cao, Y. Li, et al. 2022. "Molecular Assessment of Demersal Fish Diversity in Prydz Bay Using DNA Taxonomy." *Deep Sea Research Part II: Topical Studies in Oceanography* 202: 105140. https://doi.org/10.1016/j.dsr2.2022.105140.

Li, H., X. Miao, R. Wang, et al. 2024. "Biodiversity of Demersal Fish Communities in the Cosmonaut Sea Revealed by DNA Barcoding Analyses." *Genes* 15, no. 6: 691. https://doi.org/10.3390/genes15060691.

Liao, Y., X. Miao, R. Wang, R. Zhang, H. Li, and L. Lin. 2023. "First Pelagic Fish Biodiversity Assessment of Cosmonaut Sea Based on Environmental DNA." *Marine Environmental Research* 192: 106225. https://doi.org/10.1016/j.marenvres.2023.106225.

Liu, Y., J. C. Moore, X. Cheng, et al. 2015. "Ocean-Driven Thinning Enhances Iceberg Calving and Retreat of Antarctic Ice Shelves." *Proceedings of the National Academy of Sciences of the United States of America* 112, no. 11: 3263–3268. https://doi.org/10.1073/pnas.1415137112.

López-Farrán, Z., C. Guillaumot, L. Vargas-Chacoff, et al. 2021. "Is the Southern Crab *Halicarcinus Planatus* (Fabricius, 1775) the Next Invader of Antarctica?" *Global Change Biology* 27, no. 15: 3487–3504. https://doi.org/10.1111/gcb.15674.

Mazloff, M. R., A. Verdy, S. T. Gille, K. S. Johnson, B. D. Cornuelle, and J. Sarmiento. 2023. "Southern Ocean Acidification Revealed by Biogeochemical-Argo Floats." *Journal of Geophysical Research: Oceans* 128, no. 5: e2022JC019530. https://doi.org/10.1029/2022JC019530.

McMurdie, P. J., and S. Holmes. 2013. "Phyloseq: An R Package for Reproducible Interactive Analysis and Graphics of Microbiome Census Data." *PLoS One* 8, no. 4: e61217. https://doi.org/10.1371/journal.pone.0061217.

Mintenbeck, K., E. R. Barrera-Oro, T. Brey, et al. 2012. "Impact of Climate Change on Fishes in Complex Antarctic Ecosystems." In *Global Change in Multispecies Systems: Part I*. Vol. 46, 351–426. Elsevier. https://doi.org/10.1016/B978-0-12-396992-7.00006-X.

Miya, M. 2022. "Environmental DNA Metabarcoding: A Novel Method for Biodiversity Monitoring of Marine Fish Communities." *Annual Review of Marine Science* 14: 161–185. https://doi.org/10.1146/annurev-marine-041421-082251.

Miya, M., Y. Sato, T. Fukunaga, et al. 2015. "MiFish, a Set of Universal PCR Primers for Metabarcoding Environmental DNA From Fishes: Detection of More Than 230 Subtropical Marine Species." *Royal Society Open Science* 2, no. 7: 150088. https://doi.org/10.1098/rsos.150088.

Morley, S. A., D. K. A. Barnes, and M. J. Dunn. 2019. "Predicting Which Species Succeed in Climate-Forced Polar Seas." *Frontiers in Marine Science* 5: 507. https://doi.org/10.3389/fmars.2018.00507.

North, A. W. 1996. "Locomotory Activity and Behaviour of the Antarctic Teleost *Notothenia coriiceps*." *Marine Biology* 126: 125–132. https://doi.org/10.1007/BF00571384.

Pawlowski, J., L. Apothélo-Perret-Gentil, and F. Altermatt. 2020. "Environmental DNA: What's Behind the Term? Clarifying the Terminology and Recommendations for Its Future Use in Biomonitoring." *Molecular Ecology* 29: 4258–4264. https://doi.org/10.1111/mec.15643.

Pellichero, V., J. Sallée, S. Schmidtko, F. Roquet, and J. T. Charrassin. 2017. "The Ocean Mixed Layer Under Southern Ocean Sea-Ice: Seasonal Cycle and Forcing." *Journal of Geophysical Research: Oceans* 122, no. 2: 1608–1633. https://doi.org/10.1002/2016JC011970.

Perry, A. L., P. J. Low, J. R. Ellis, and J. D. Reynolds. 2005. "Climate Change and Distribution Shifts in Marine Fishes." *Science* 308, no. 5730: 1912–1915. https://doi.org/10.1126/science.1111322.

R Core Team. 2024. "The R Project for Statistical Computing." https://www.r-project.org.

Riekkola, L., V. Andrews-Goff, A. Friedlaender, R. Constantine, and A. N. Zerbini. 2019. "Environmental Drivers of Humpback Whale Foraging Behavior in the Remote Southern Ocean." *Journal of Experimental Marine Biology and Ecology* 517: 1–12.

14724642, 2025, 7, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ddi.70053 by Kobe University, Wiley Online Library on [23/09/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Rignot, E., S. Jacobs, J. Mouginot, and B. Scheuchl. 2013. "Ice-Shelf Melting Around Antarctica." *Science* 341, no. 6143: 266–270. https://doi.org/10.1126/science.1235798.

Roblet, S., F. Priouzeau, G. Gambini, et al. 2024. "From Sight to Sequence: Underwater Visual Census vs Environmental DNA Metabarcoding for the Monitoring of Taxonomic and Functional Fish Diversity." *Science of the Total Environment* 956, no. 15: 177250. https://doi.org/10.1016/j.scitotenv.2024.177250.

Rodriguez-Ezpeleta, N., O. Morissette, C. W. Bean, et al. 2021. "Trade-Offs Between Reducing Complex Terminology and Producing Accurate Interpretations From Environmental DNA: Comment on 'Environmental DNA: What's Behind the Term?' By Pawlowski Et al., (2020)." *Molecular Ecology* 30: 4601–4605. https://doi.org/10.1111/mec.15942.

Rogers, A. D., B. Frinault, D. Barnes, et al. 2020. "Antarctic Futures: An Assessment of Climate-Driven Changes in Ecosystem Structure, Function, and Service Provisioning in the Southern Ocean." *Annual Review of Marine Science* 12: 87–120. https://doi.org/10.1146/annurev-marine-010419-011028.

Sahade, R., C. Lagger, L. Torre, et al. 2015. "Climate Change and Glacier Retreat Drive Shifts in an Antarctic Benthic Ecosystem." *Science Advances* 1, no. 10: e1500050. https://doi.org/10.1126/sciadv.1500050.

Schmidtko, S., L. Stramma, and M. Visbeck. 2017. "Decline in Global Oceanic Oxygen Content During the Past Five Decades." *Nature* 542: 335–339. https://doi.org/10.1038/nature21399.

Sergi, S., A. Baudena, C. Cotté, M. Ardyna, S. Blain, and F. d'Ovidio. 2020. "Interaction of the Antarctic Circumpolar Current With Seamounts Fuels Moderate Blooms but Vast Foraging Grounds for Multiple Marine Predators." *Frontiers in Marine Science* 7: 416. https://doi.org/10.3389/fmars.2020.00416.

Simpson, S. D., S. Jennings, M. P. Johnson, et al. 2011. "Continental Shelf-Wide Response of a Fish Assemblage to Rapid Warming of the Sea." *Current Biology* 21, no. 18: 1565–1570. https://doi.org/10.1016/j.cub.2011.08.016.

Swart, N. C., S. T. Gille, J. C. Fyfe, and N. P. Gillett. 2018. "Recent Southern Ocean Warming and Freshening Driven by Greenhouse Gas Emissions and Ozone Depletion." *Nature Geoscience* 11: 836–841. https://doi.org/10.1038/s41561-018-0226-1.

Taberlet, P., A. Bonin, L. Zinger, and E. Coissac. 2018. *Environmental DNA: For Biodiversity Research and Monitoring*. Oxford University Press.

Takeuchi, A., T. Sado, R. O. Gotoh, S. Watanabe, K. Tsukamoto, and M. Miya. 2019. "New PCR Primers for Metabarcoding Environmental DNA From Freshwater Eels, Genus Anguilla." *Scientific Reports* 9: 7977. https://doi.org/10.1038/s41598-019-44402-0.

Trokhymets, V., O. Savytskiy, A. Zinkovskyi, et al. 2022. "Species Composition, Distribution and Relative Abundance of the Inshore Fish Community Off the Argentine Islands, Bellingshausen Sea." *Polar Biology* 45: 845–855. https://doi.org/10.1007/s00300-022-03040-5.

Van de Putte, A. P., G. D. Jackson, E. Pakhomov, H. Flores, and F. A. M. Volckaert. 2010. "Distribution of Squid and Fish in the Pelagic Zone of the Cosmonaut Sea and Prydz Bay Region During the BROKE-West Campaign." *Deep Sea Research Part II: Topical Studies in Oceanography* 57, no. 9–10: 956–967. https://doi.org/10.1016/j.dsr2.2008.02.015.

Wickham, H. 2011. "ggplot2." *WIREs Computational Statistics* 3, no. 2: 180–185. https://doi.org/10.1002/wics.147.

Williams, G. D., L. Herraiz-Borreguero, F. Roquet, et al. 2016. "The Suppression of Antarctic Bottom Water Formation by Melting Ice Shelves in Prydz Bay." *Nature Communications* 7: 12577. https://doi.org/10.1038/ncomms12577.

Wu, L., Q. Wu, T. Inagawa, J. Okitsu, S. Sakamoto, and T. Minamoto. 2023. "Estimating the Spawning Activity of Fish Species Using Nuclear and Mitochondrial Environmental DNA Concentrations and Their Ratios." *Freshwater Biology* 68, no. 1: 103–114. https://doi.org/10.1111/fwb.14012.

Wu, Q., K. Kawano, T. Ishikawa, et al. 2019. "Habitat Selection and Migration of the Common Shrimp, *Palaemon paucidens* in Lake Biwa, Japan – An eDNA-Based Study." *Environmental DNA* 1, no. 1: 54–63. https://doi.org/10.1002/edn3.6.

Wu, Q., M. K. Sakata, D. Wu, H. Yamanaka, and T. Minamoto. 2021. "Application of Environmental DNA Metabarcoding in a Lake With Extensive Algal Blooms." *Limnology* 22, no. 3: 363–370. https://doi.org/10.1007/s10201-021-00663-1.

Yao, M., S. Zhang, Q. Lu, et al. 2022. "Fishing for Fish Environmental DNA: Ecological Applications, Methodological Considerations, Surveying Designs, and Ways Forward." *Molecular Ecology* 31, no. 20: 5132–5164. https://doi.org/10.1111/mec.16659.

Zhang, R., P. Song, H. Li, et al. 2022. "Spatio-Temporal Characteristics of Demersal Fish Community in the Chukchi and Northern Bering Seas: Significant Distributional Records and Interannual Variations in Species Composition and Biodiversity." *Polar Biology* 45: 259–273. https://doi.org/10.1007/s00300-021-02980-8.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.

14724642, 2025, 7, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ddi.70053 by Kobe University, Wiley Online Library on [23/09/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License