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RESEARCH

What's inside the net? insights into fish bycatch diversity in the Antarctic krill fishery

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Abstract

An ecosystem-based approach to fishery management requires, inter alia, knowledge of fishery impacts on both target and non-target species, as well as the wider ecosystem. To support management of the Antarctic krill fishery, we present a robust reference dataset for identifying fish species caught as bycatch. By combining morphological and molecular taxonomic identification, 53 fish species in 44 genera and 11 families were confidently identified. Our dataset extends the DNA barcode library of Sub-Antarctic and Antarctic fish species and provides a foundation for developing an enhanced identification guide for larval fish to be used by observers on board krill fishing vessels. Phylogenetic relationships were inferred from two commonly used barcode markers, the mitochondrial *cox1* and the non-coding control region. We observed clear phylogenetic relationships, highlighting coherent placements of notothenioids, myctophids, Aulopiformes, Gadiformes and Zoarcoidei. The results suggest a discrepancy between observer-based and genetic identifications, with 20.6% of records representing misidentifications in the fishing seasons 2021/2022 and 2022/2023.

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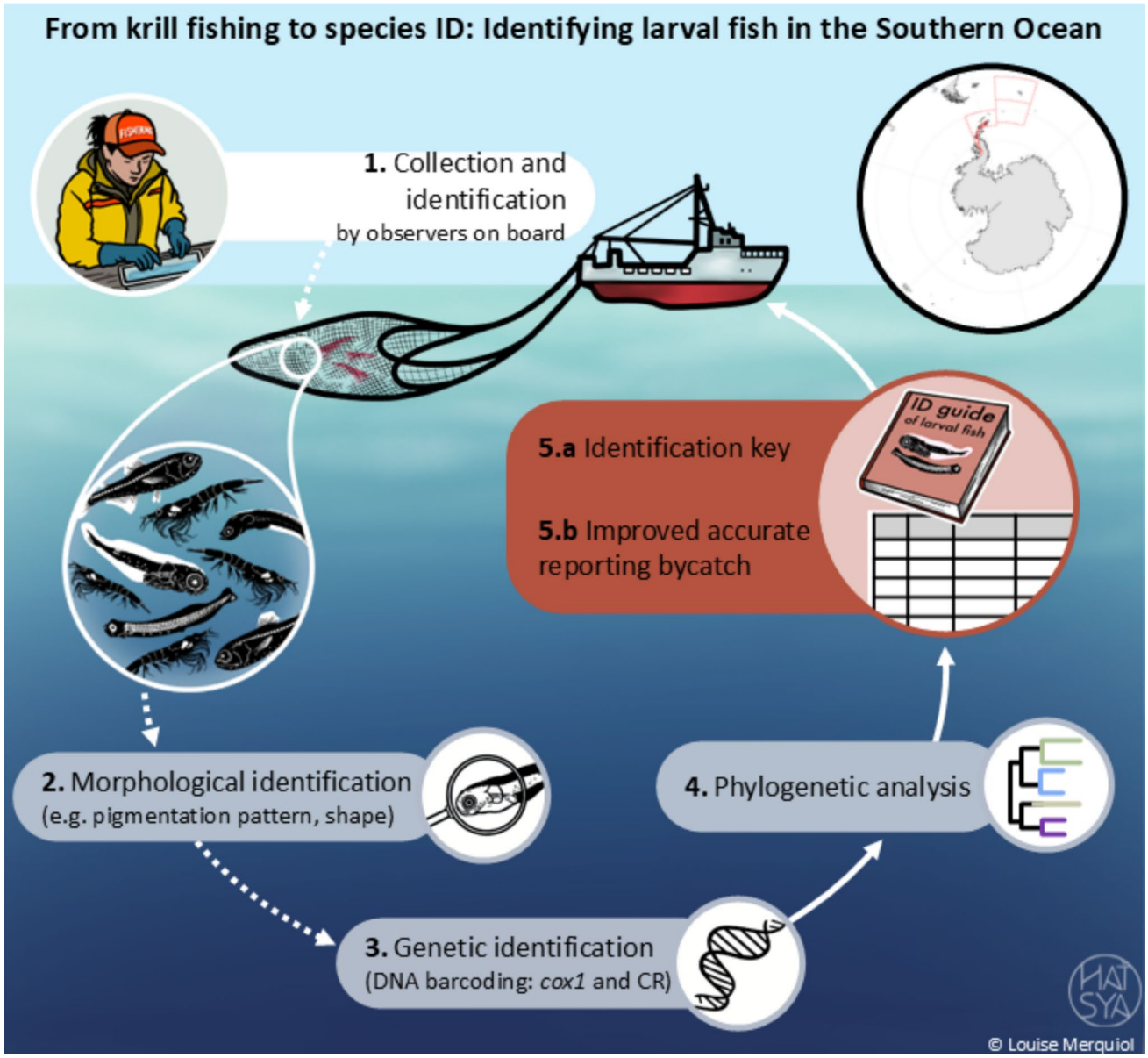
Graphical Abstract



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Keywords *Cox1* · DNA barcoding · Fisheries · Larval fish · Southern Ocean

Introduction

Global demand for marine-related products is increasing as human populations grow, placing stress on the marine ecosystem; through industries like fishing, which extract resources to satisfy human protein and micronutrient requirements (Hicks et al. 2019). In 2022, the world's production of aquatic animals reached 185.4 million tonnes, of which 91 million tonnes were from global capture fisheries. Of this, 89% was for human consumption and 11% for production of fishmeal and fish oil used in farming, pet food and pharmaceutical industries (FAO 2024a). Despite the implementation of international frameworks such as the *Code of Conduct for Responsible Fisheries* (FAO 1995) and the *International Guidelines on Bycatch Management and Reduction of Discards* (FAO 2011), bycatch and discards remain persistent challenges in global fisheries. These issues continue amid rapid

technological advances in fishing gear (He et al. 2021; Sala and Richardson 2023; FAO 2024b), strengthened efforts to combat illegal, unreported and unregulated fishing (FAO 2001, 2023), and international agreements promoting the sustainable use of aquatic ecosystems (FAO 2022; WTO 2022). When occurring at unsustainable levels, the mortality of non-target species, including impacts from abandoned, lost or discarded fishing gear and fish discards (the proportion of the total catch returned to the sea dead or alive (FAO 2011)), undermines the long-term sustainability of fisheries and the maintenance of biodiversity, posing ongoing challenges to global capture fisheries production (Davies et al. 2009; Lively and McKenzie 2023; FAO 2024a). As previously unexploited parts of the ocean are increasingly considered as new fishing avenues, close attention and diligent mitigation measures are required. One example is the mesopelagic zone (200–1000 m depth), where lanternfishes (Myctophidae) are of increasing interest due to the estimated biomass and potential fishery value (Valinassab et al. 2007; Schadeberg et al. 2023; Vastenhound et al. 2023; Prellezo et al. 2024). Bycatch can occur across multiple life-history stages and varies in space and time, meaning the risk of bycatch is not uniform across a species' life or distributional range. Consequently, as fisheries expand in size (number of vessels and/ or ability to extract target resources) or spatial coverage, accurate reporting of catch composition, biomass, capture location, and life-history stage is essential to assess environmental impacts and inform effective bycatch management strategies.

Antarctic krill (*Euphausia superba*) has been harvested in the Southern Ocean since 1973, with fisheries operating in three principal areas of the Southwest Atlantic Sector (Area 48) (Constable et al. 2002; Nicol et al. 2011). The krill fishery moves seasonally depending on sea ice extent and operational constraints, typically starting in the South Orkneys and the Antarctic Peninsula and moving north to South Georgia during the austral winter (Kawaguchi et al. 2006; Cruz et al. 2018). Concerns in relation to fisheries harvesting this resource and potential competition with krill-dependent predators prompted the establishment of the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR), which has responsibility for managing Southern Ocean fisheries (Press and Constable 2022). CCAMLR establishes conservation measures utilising a precautionary approach to manage the Antarctic krill fishery. Conservation Measures 51–01 (a precautionary catch limit) and 51–07 (a trigger level) were implemented in Subareas 48.1 to 48.4. However, the expiry of CM 51–07 (CCAMLR 2022) and a lack of agreement on a suitable replacement measure are likely to lead to greater spatial concentration of krill fishing activities. Even with these measures in place, concerns in relation to fish bycatch are growing (Jones 2022; Krafft et al. 2022). There is a pressing requirement to identify fish at different life-history stages so that accurate bycatch estimates can be established.

The conservative approach to the management of the krill fishery by CCAMLR requires 100% observer coverage on all fishing vessels (Kawaguchi and Nicol 2021; CCAMLR 2025a: Conservation Measure 56–01). Observers undertake routine sampling of krill and identify bycatch species. However, determining the nature and magnitude of fish bycatch remains latent concerns. Because the fishing gear for krill has both a large net size (106 to 188 m) and fine mesh (11 to 20 mm) (CCAMLR 2026), and the fishing depth can extend as deep as 200 m (Krafft et al. 2016; Trathan et al. 2021), fishing for krill inevitably results in fish bycatch (Rembiszewski et al. 1978; Everson et al. 1992). Moreover, with the recent increase in krill catches, finfish bycatch has significantly increased (Kock and Jones 2014; Jones 2022; Krafft et al. 2022), particularly in the southern Scotia Sea (Jones 2022). Whilst observers have provided consistent reports, there is room for improvement, and one of the pressing issues is the correct identification of fish species, particularly larval and juvenile stages, which make up a large proportion of the bycatch (CCAMLR Secretariat 2016, 2017, 2018; Polanowski et al. 2018). Over the course of the year, different life-history stages of fish are caught, meaning that the risk of capture of a particular life-history stage may not be equal across the areas fished (Slosarczyk 1983; North 1987; Iwami et al. 2011). This is compounded by difficulty in identifying the larvae of species in families such as the Channichthyidae and Nototheniidae, which are routinely caught in the bycatch (CCAMLR Secretariat 2022).

Accurate species identification is crucial to discovering the true extent of life's diversity. Taxonomy, as the science that delimits the units of life, has evolved from classical analysis of morphological traits towards an integrative approach, whereby species identification and classification are ascertained from multiple and complementary perspectives (Dayrat 2005; Padial et al. 2010; Goulding and Dayrat 2016), including phylogeography, population genetics and ecology. As part of the integrative taxonomy approach, molecular techniques are viewed as efficient and reliable methods to resolve taxonomic uncertainties, among these is the use of DNA barcodes. The routine application of molecular techniques for the identification of species based on mitochondrial markers facilitates the identification process beyond morphology-based assignments and clarifies the taxonomic status of species of close resemblance. One of the most suitable mitochondrial markers used in taxonomic discrimination of species is *Cytochrome c oxidase subunit* 1 or *cox1* (COI, CO1). This genetic marker is supported by a large database of curated reference sequences from which taxonomic

assignment can be established. It is highly efficient in discriminating among species and has the potential to distinguish closely related species (Rock et al. 2008; Smith et al. 2012; Silva Rodrigues et al. 2017; Christiansen et al. 2018; Cao et al. 2022). Alongside *cox1,* the non-coding control region not only discriminates between species but also has the potential to highlight genetic differences between populations, due to the variation in length, and DNA base changes in this region across many animal species, including fish, where the number of short repetitive elements can facilitate the distinction between groups of fish (O'Bryan et al. 2010; Satoh et al. 2016; Bronstein et al. 2018; Peng et al. 2023).

There is a requirement to develop appropriate life-history stage-specific identification materials that enable accurate identification of bycatch. This will improve CCAMLR reporting and advance spatial and temporal understanding of the bycatch risk across life-history stages to inform management decisions. Here, we address this requirement by using an integrative taxonomy approach, whereby morphological identification was cross-referenced with genetic identification. Specifically, we employed two mitochondrial markers, *cox1* and the control region, for the genetic identification of species, and compared these with morphological identifications provided by observers on board krill fishing vessels. In addition, we provide an identification toolbox consisting of group- and species-amplifying PCR primers for the identification of fish species in Area 48 of the Southern Ocean, along with a carefully curated reference sequence dataset to enhance public DNA references for marine species.

Materials and methods

Sampling and morphological identification

Fish were collected from fishing operations during the 2021/2022 and 2022/2023 seasons, covering the austral winter months, in statistical subareas 48.1, 48.2 and 48.3 in the Southwest Atlantic Sector of the Southern Ocean (Fig. 1). Fishery observers on board five fishing vessels, two conventional trawlers and three with a continuous pumping system, sorted and identified all fish bycatch within a 25 kg krill sample at least once per day (see Supplementary material Table S1 for fishing gear). Specimens were identified following the identification material by Iwami and Naganobu (2007). For each species (or suspected species), larval, juvenile, and adult fish were retained. Juvenile and adult fish were stored frozen at -20 °C, whilst larvae were preserved in 90% ethanol to maintain morphological integrity for photographic documentation. Larval samples were kept at -20 °C

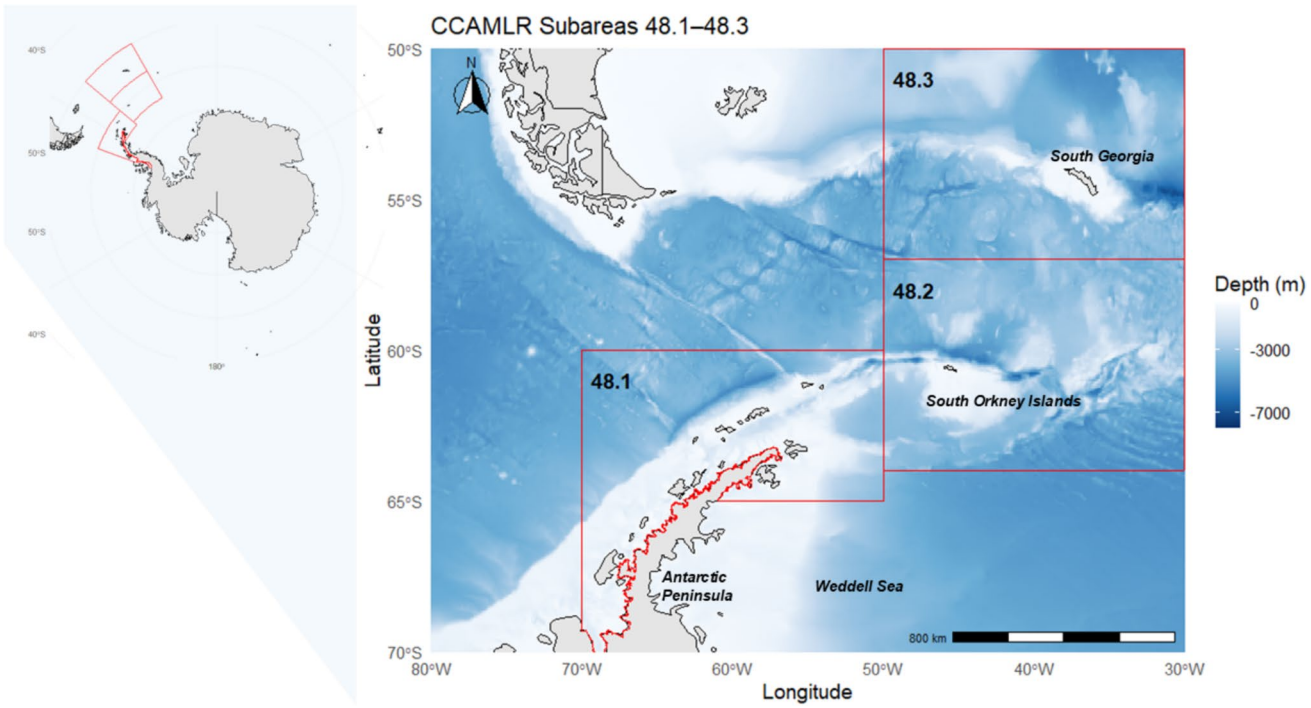

Fig. 1 Map of the study area showing CCAMLR Subareas 48.1 to 48.3 within area 48, where the krill fishery actively operates. Red lines indicate the boundaries of each subarea, including 48.1 (Antarctic Peninsula and South Shetland Islands), 48.2 (South Orkney Islands) and 48.3 (South Georgia)

during transport to the laboratory, and DNA extraction was conducted shortly after arrival. Additionally, the biological archive at the British Antarctic Survey (BAS) was examined for larval samples of species reported as bycatch but not necessarily observed in the fishery observer samples. These archival samples included specimens collected during scientific surveys and other commercial fishing activities.

In the laboratory, a maximum of ten replicates per putative species were subsampled for DNA by making a small incision on the right side of the body to dissect about 25 mg of muscle tissue. The dissected tissue was bisected, and 12.5 mg of tissue was used for DNA extraction. Specimens were identified to the lowest taxonomic level using identification keys by Effremenko (1983) and Kellermann and North (1989) for larvae, and by Gon and Heemstra (1990) for juveniles and adults. Fish were measured to the nearest millimetre (total and standard lengths) and photographed using a Nikon Z camera (Model N1929) fitted with a macro lens (Nikkor Z mount MC 50 mm f/2.8 or a Laowa 25 mm f2.8 2.5–5 × ultra) mounted on a copy stand.

DNA amplification, sequencing and analysis

Genomic DNA (gDNA) was extracted using either the PureLink™ Genomic DNA Mini Kit (Invitrogen, Waltham, MA, USA) or the DNeasy® Blood and Tissue Kit (Qiagen Ltd., West Sussex, UK), following the manufacturer's instructions. The extracted gDNA was eluted in 50–70 µl of elution buffer and stored at -20 ˚C before amplification of the mitochondrial *cox1* gene and control region by polymerase chain reaction (PCR).

PCR amplification was performed using 22 species-targeting primers for *cox1* and 22 for the control region (see Supplementary material Table S2-S3 and Figure S1 for primer testing and validation). Given the close phylogenetic relationships within the Notothenioidei, different species belonging to the same genus could be amplified with the same primer pairs. The *cox1* primers were modified with non-degenerate primer tails (Goodall-Copestake 2014) attached to the 5' end to serve as priming sites for Sanger sequencing. All PCR reactions had a total volume of 15 µl, containing 5.9 µl of ultrapure water, 7.5 µl of 2 × MyTaq HS master mix (Meridian Bioscience, Bioline Reagents Ltd, UK), 0.3–0.5 µM of each forward and reverse primer and 1 µl of DNA template (mean concentration of 50 ng/ul DNA). The thermocycling conditions for *cox1* included an initial denaturation at 95 °C for 2 min, followed by 38 cycles at 95 °C for 20 s, 50 °C for 30 s, 72 °C for 1.5 min and a final extension at 72 °C for 1 min. For the control region, the protocol included an initial denaturation at 95 °C for 5 min, followed by 38 cycles at 95 °C for 20 s, 50–55 °C for 30 s, 72 °C for 2 min and final extension at 72 °C for 1 min.

PCR products were visualised by gel electrophoresis before purification using ExoSAP-IT Express (Appliedbiosystems, Thermo Fisher Scientific, Santa Clara, CA, USA). Purified *cox1* PCR products (~ 700 bp fragments) were sent to Eurofins Genomics UK (Wolverhampton, UK) for Sanger sequencing. Control region amplicons were sequenced in-house using the Oxford Nanopore Technology (ONT) MinIon Mk1B (MIN-101B) and the MinKnow v23.07.15 sequencing platform. Library preparation was conducted using the ONT Native Barcoding Kit 96 V14 chemistry (SQK-NBD114.96) with Q20 + modal raw read accuracy, following the manufacturer's instructions, and using default experimental settings for all sequencing runs. Libraries were sequenced on R10.4.1 Flongle Flow Cells. The data processing toolkit used for base-calling were Dorado v7.3.9. Basecalling was performed using the High Accuracy (HAC) base-calling model, with a minimum Q-score of 9, and a read length between 200 and 1500 bp was used for filtering raw reads. Filtered reads were demultiplexed, and primer trimming was enabled in each sequencing run.

The downstream analysis of *cox1* sequencing data was performed using Geneious Prime v.2024.0.5 (GraphPad Software LLC) to inspect electropherograms for base quality scores, primer trimming, and contig assembly using the 'Map to Reference' function. For species without a reference sequence, a novel sequence was generated by the 'de novo' function. For the control region, the raw reads were basecalled again using the HAC algorithm, and the same Q-score and read length cut-offs were applied for filtering before demultiplexing; sequences successfully classified to a barcode were further processed in Geneious using the "de novo" function to create consensus sequences per barcode, a minimum of 30 reads supporting the consensus sequence was used as a cut off (Sahlin et al. 2021). Sequence alignment followed the Workflow Alignment (WF-Alignment) in the EPI2ME Agent platform (v. 3.7.3), using a custom reference database compiled from all available mitogenomes and control region sequences in GenBank. This reference database was uploaded to EPI2ME under the dataset '*Fish mitogenomes and D-loop*' (ID 450871). Taxonomic assignments of individual barcodes were manually verified by mapping sequences to a reference using the 'Map to Reference' function in Geneious. All taxonomic assignments were cross-checked against the NCBI sequence database using the BLAST search tool and the *megablast* algorithm. Sequences with ≥ 98% similarity to a reference sequence were classified as the same species (Murphy et al. 2017), whilst those with < 98% but ≥ 95% similarity were assigned to the same genus (Ratnasingham and Hebert 2013; Cao et al. 2022).

To investigate phylogenetic relationships of the sequences obtained from observer samples, both Neighbour-joining

(NJ) and Maximum-Likelihood (ML) trees were reconstructed for *cox*1 and the control region. Multiple sequence alignment was performed using MUSCLE v5.1 (Edgar 2004) and used as input for both tree-building methods. The optimal nucleotide substitution model was determined using JModeltest 2.1.10 v20160303 (Guidon and Gascuel 2003; Darriba et al. 2012) based on Akaike's Information Criterion corrected for small sample sizes (AICc).

NJ trees were constructed using the Tamura-Nei (TN93) model (Tamura and Nei 1993), with 1,000 bootstrap replicates and a 90% support threshold for resampling the consensus tree. ML trees were also built using the TN93 model with 1,000 bootstrap replicates and fixed gamma shape parameters. All alignments and phylogenetic analyses were performed in Geneious Prime v.2024.0.5.

Results

Morphological identification by fishery observers

Between 2021/2022 and 2022/2023, a total of 664 fish specimens were collected by observers from the 25 kg bycatch sample. These included 60 larval fish specimens, 393 larvae transitioning to juveniles and 216 late-stage juveniles and adults. Observers identified 35 species in 28 genera and 10 families. Of the total number of samples, 20.4% came from subarea 48.1, 59.2% from subarea 48.2 and 20.4% from subarea 48.3.

Of the total specimens, 26 were identified only to the family or genus level, with myctophids being the most numerous. Difficulty in identification was noted within the Myctophiformes, particularly the genera *Electrona, Gymnoscopelus* and *Protomyctophum.* Other frequently unresolved groups included larval icefish (Perciformes, Channichthyidae), grenadiers (Gadiformes, Macrouridae), eel cods (Gadiformes, Muraenolepididae) and lanternfishes (Myctophiformes, Myctophidae), which were broadly classified as Icefish, Macrouridae, Muraenolepididae and Myctophidae, respectively. Additionally, six specimens remained unidentified and were classified as unknown.

In descending order of species richness, the taxonomic breakdown of samples identified by observers included 9 species in 8 genera of icefishes (Channichthyidae), 9 species in 7 genera of notothens (Nototheniidae) and 7 species in 4 genera of lanternfishes (Myctophidae). Additionally, 3 species in 2 genera of dragonfishes (Bathydraconidae), 2 species in 2 genera of barracudinas (Paralepididae) and 1 species in each of the following families were identified: Anotopteridae, Artedidraconidae, Centrolophidae, Scopelarchidae and Zoarcidae.

Table 1 Breakdown of samples selected for genetic identification by subarea and by fishing vessel type

	Subarea		
	48.1	48.2	48.3
Conventional	28	67	67
Continuous	33	36	113
Total	61	103	180

Genetic identification

A total of 344 samples were selected for genetic identification through amplification and sequencing of the mitochondrial *cox1* and control region. Samples were selected at random from each of the subareas and from both conventional and continuous trawlers (Table 1).

*Cox*1 fragments were obtained from all samples, whilst for the control region the top 20 most abundant bycatch species were selected for sequencing, resulting in 198 sequenced samples for control region. The *cox*1 sequences showed no insertions, deletions or stop codons and ranged from 615 to 639 bp with an average base composition of $A = 22\%$, $C = 29.4\%$, $G = 19.2\%$, $T = 29.4\%$; whilst control region sequences ranged from 242 to 1223 bp with an average base composition of $A = 29.3\%$, $C = 23.9\%$, $G = 17.0\%$, $T = 28.9\%$. The sequencing run outputs and sequencing depth per family are shown in Tables 2 and 3, whilst information on the sequencing run and flow cell performance is provided in Supplementary material Fig. S2.

The total fish diversity comprised 53 species in 44 genera and 11 families. Nototheniidae (11 species), Channichthyidae (9 species) and Myctophidae (4 species) were the most diverse. Sequences were deposited in GenBank under Bioproject PRJNA1270765. The *cox*1 sequences for *Notolepis annulata* (Aulopiformes, Paralepididae) and *Parachaenichthys georgianus* (Perciformes, Channichthyidae) are new additions to GenBank, as no reference sequences were previously available for these species. Similarly, control region sequences for *Lindbergichthys nudifrons* (Perciformes, Nototheniidae), *Magnisudis prionosa* (Aulopiformes, Alepisauridae), *Paradiplospinus gracilis* (Scombriformes, Gempylidae), *Achiropsetta tricholepis* (Pleuronectiformes, Achiropsettidae) and *Mancopsetta maculata* (Pleuronectiformes, Achiropsettidae) are also new additions.

Phylogenetic relationships were illustrated in two trees: the Neighbour-Joining and Maximum Likelihood, both of which showed similar topologies and consistently supported well-differentiated branches for major families such as Channichthyidae, Nototheniidae and Myctophidae. However, discrepancies were observed in the branching patterns of genera within less diverse families, such as Paralepididae (Supplementary material Fig. S3-S4). Despite these differences, individuals clustered correctly by species with their

Table 2 Sequencing run outputs and reads retained after quality filtering

Run name	Flow cell type/kit type	Sequencing output		After quality filtering and demultiplexing		
		# of reads	Mean Q-score	# of reads	Mean Q-score	Percentage retained (%)
Library 1: samples 1–48	FLO-FLG114/ SQK-NBD 114–96	137,187	12.23	102,900	15.65	75
Library 2: samples 49–144	FLO-FLG114/ SQK-NBD 114–96	187,970	12.00	134,732	15.52	72
Library 3: samples 145–198	FLO-FLG114/ SQK-NBD 114–96	278,160	14.5	235,475	18.00	85

Table 3 Sequencing depth per family

Order	Family	Total number of reads	Total no of passed reads	%passed reads
Pleuronectiformes	Achiropsettidae	23,090	8,572	37.1
Aulopiformes	Alepisauridae	51,910	38,038	73.3
Perciformes	Bathydraconidae	143,320	114,789	80.1
Perciformes	Channichthyidae	139,375	111,870	80.3
Scombriformes	Gempylidae	58,930	51,552	87.5
Perciformes	Harpagiferidae	22,250	20,087	90.3
Myctophiformes	Myctophidae	29,520	24,667	83.6
Perciformes	Notothenioidea	111,342	82,304	73.9
Aulopiformes	Paralepididae	23,580	21,229	90.0

respective reference sequences in both trees. To aid interpretation, the phylogenetic trees (Fig. 2) include a subset of samples that were morphologically misidentified by observers. For the complete set of phylogenetic trees, encompassing all samples, refer to the Supplementary material Fig. S5 and S6.

The resulting phylogenetic tree based on *cox*1 sequences (Fig. 2a) strongly supports the monophyly of the order Notothenioidei, a diverse group of Antarctic fishes encompassing the families Channichthyidae, Bathydraconidae, Harpagiferidae and Nototheniidae. High bootstrap support values indicated well-resolved relationships within this clade and reinforced the accurate taxonomic placement of previously misidentified samples, which clustered reliably within their corresponding family and species-level reference sequences. Other major groups, such as Myctophiformes (Myctophidae), Aulopiformes (Paralepididae) and Gadiformes (Moridae, Muraenolepididae), formed distinct, well-supported clades, highlighting clear evolutionary divergence and clustering separately from Notothenioidei.

Similarly, the phylogeny based on control region sequences (Fig. 2b) strongly supports the monophyly of Notothenioidei, with individuals clustering within their respective families alongside their reference sequences, confirming accurate taxonomic classification. However, the placement of the Myctophidae reference sequence (ELN_AP0122) and the sample (ELN_ELC_0_493) was unexpected, as they did not cluster together. This discrepancy was further examined using the complete dataset (Supplementary material Fig. S4 and S6) and a cross-check of the *Electrona antarctica* specimen using the *cox*1 gene to confirm the correct taxonomic identification of the sample as *E. antarctica*.

Genetic identification and observers IDs

Overall, fishery observers correctly identified 70.1% of the analysed bycatch. Misidentifications accounted for 20.6%, whilst 3.5% of the specimens were identified only to the genus level, and 5.8% remained unknown. Spatial variation in identification accuracy was evident across the three subareas. In Subarea 48.1, correct identifications accounted for 81.7% of the samples, 16.7% were misidentified, and 1.0% identified to genus level. Subarea 48.2 showed the highest rate of misidentifications, comprising nearly half of the samples (46.6%), whilst correct identifications accounted for 48.5%, genus-level identification for 1.9% and unknowns for 2.9%. Subarea 48.3 had 78.5% correct identifications with only 7.2% misidentified, 5.0% identified to genus level and

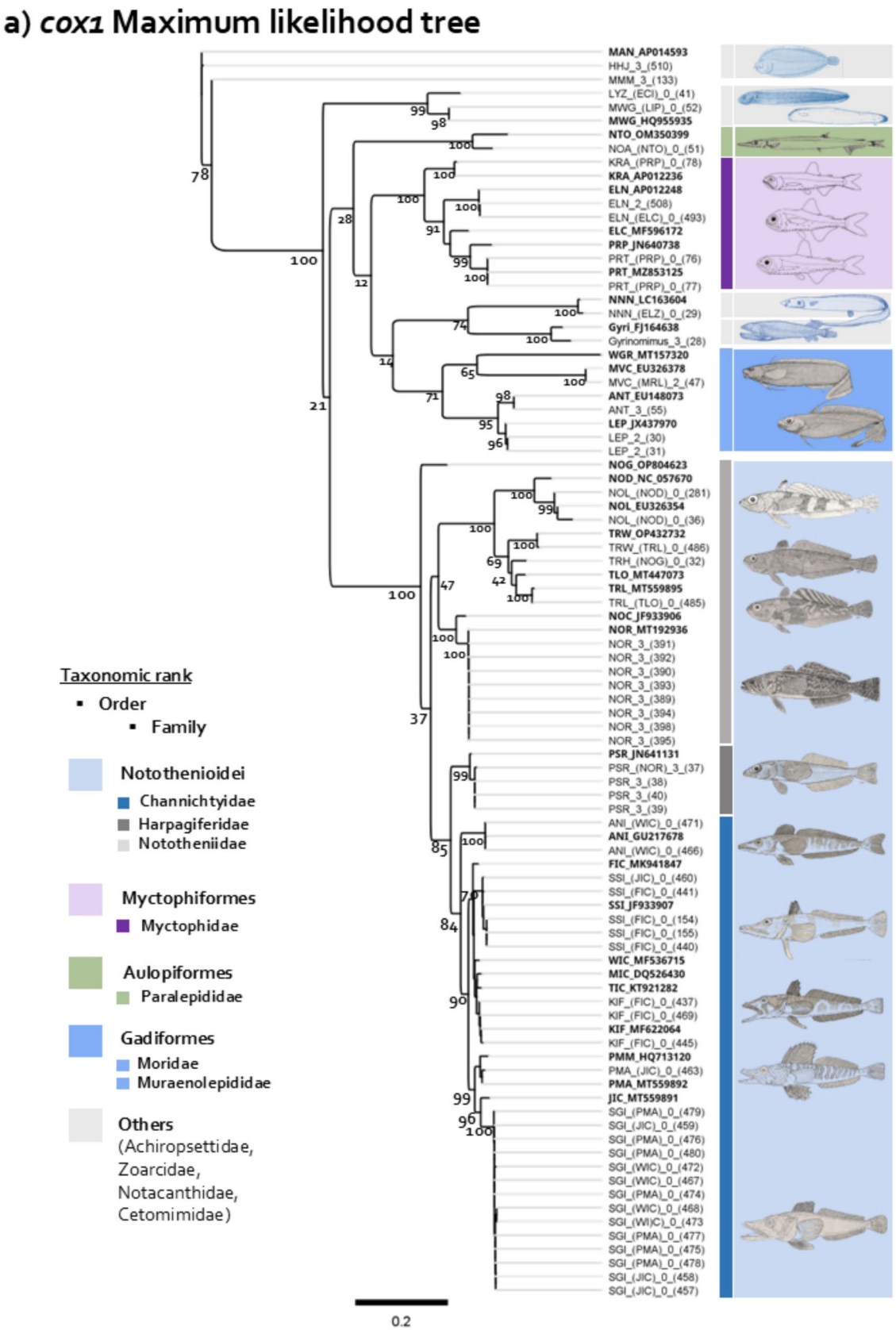

Fig. 2 Maximum Likelihood (ML) phylogenetic trees based on mitochondrial *cox1* and control region sequences. The scale bar represents genetic distance. Bootstrap support values are shown at key nodes. Fish species are colour-coded according to their taxonomic classification at the family level, as indicated in the legend. Reference sequences in bold. **a** In the *cox1* ML phylogeny (unrooted), four orders are differentiated and include Notothenioidei (blue shades) Myctophiformes (purple), Aulopiformes (green), Gadiformes (dark blue) and other taxa (grey). **b** Control region ML phylogeny (unrooted) differentiated between members of Notothenioidei and Myctophiformes. Sample name was coded as follows: corrected species code_misidentification_species code_ misidentification score (0–3) _sample number, e.g.: ANI_WIC_0_30. See supplementary material Table S4 for species codes

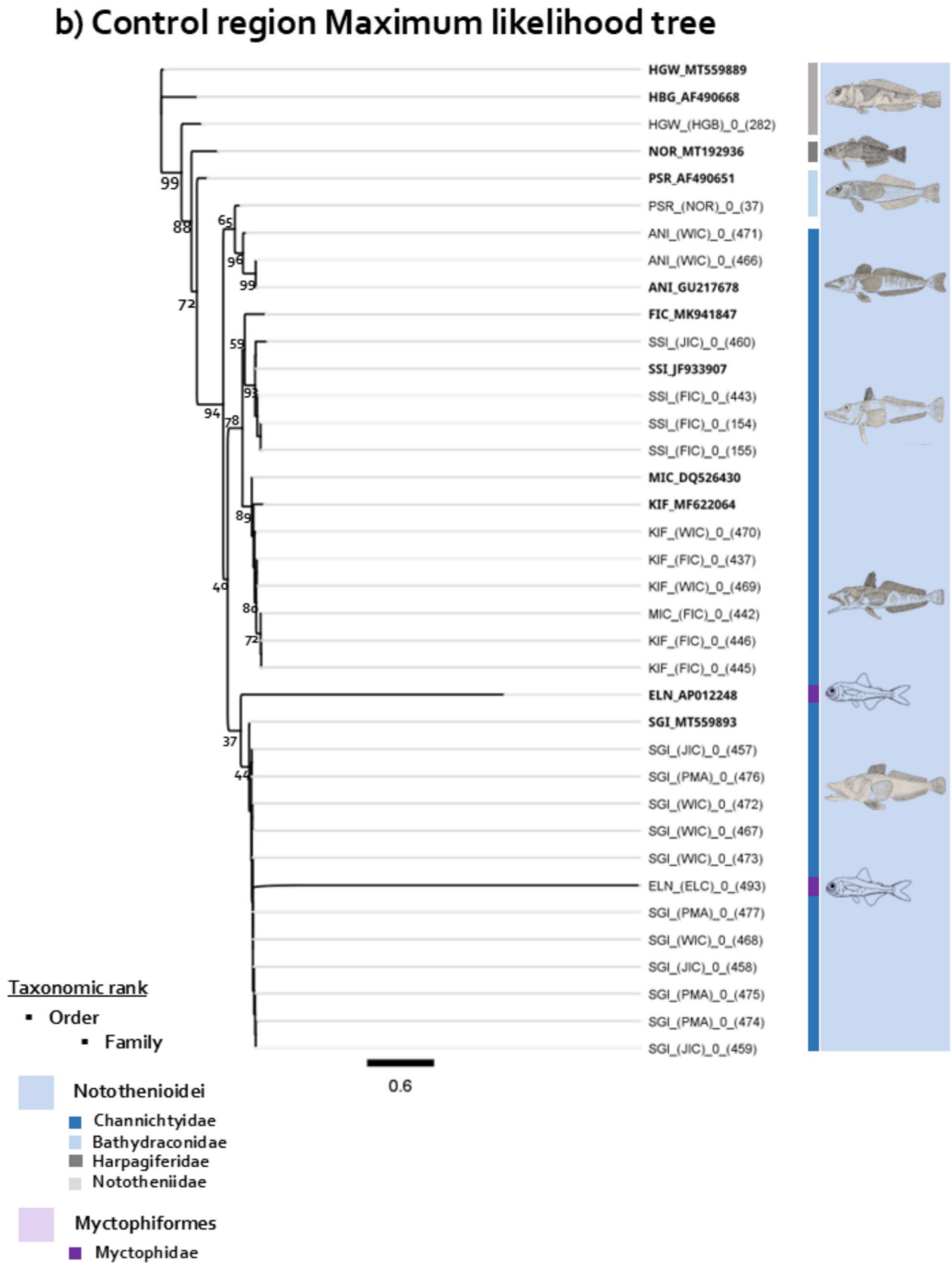

Fig. 2 (continued)

Table 4 Comparison of genetic and observers' identifications of fish specimens collected as bycatch

a)		Genetic ID ($n=144$)								
	Species code	ANI	SSI	SGI	KIF	WIC	FIC	JIC	PMA	TIC
Observers ID	ANI	**39**								
	SSI		**17**				**2**			
	SGI			**16**						
	KIF				**14**					
	WIC	**3**	**1**	**4**	**2**	**12**				
	FIC		**5**		**2**		**7**			
	JIC		**1**	**3**				**4**	**1**	
	PMA			**7**					**3**	
	TIC								**1**	**0**

b)		Genetic ID ($n=71$)							
	Species code	NOL	NOG	NOD	TRH	TRL	TRW	TLO	ANS
Observers ID	NOL	**33**	**1**			**2**			
	NOG	**2**	**8**		**1**				
	NOD			**5**					
	TRH				**6**				
	TRL					**3**	**1**		
	TRW					**1**	**1**		
	TLO							**0**	
	ANS								**7**

c)		Genetic ID ($n=66$)							
	Species code	ELN	ELC	KRA	PRM	PRT	PRP	GYN	GYR
Observers ID	ELN	**22**	**2**						
	ELC	**9**	**6**		**1**				
	KRA			**10**					
	PRM				**1**				
	PRT					**1**			
	PRP			**3**			**0**		
	GYN							**10**	
	GYR								**1**

Observers recorded identifications for species of Channichthyidae (a), Nototheniidae (b) and Myctophidae (c). Bold values indicate agreement with genetic identification, red values indicate disagreement. *C. gunnari* (ANI), *C. aceratus* (SSI), *Ps. georgianus* (SGI), *C. rastrospinosus* (KIF), *C. wilsoni* (WIC), *C. antarcticus* (FIC), *N. ionah* (JIC), *P. macropterus* (PMA), *C. hamatus* (TIC), *N. larseni* (NOL), *G. gibberifrons* (NOG), *L. nudifrons* (NOD), *T. hansoni* (TRH), *T. eulepidotus* (TRL), *T. newnesi* (TRW), *T. loennbergii* (TLO), *P. antarcticum* (ANS), *E. antarctica* (ELN), *E. carlsbergi* (ELC), *K. anderssoni* (KRA), *P.bolini* (PRM), *P. tenisoni* (PRT), *P. parallelum* (PRP), *G. nicholsi,* (GYN), *G. braueri* (GYR).

9.4% classified as unknown (Table 4; Supplementary material Fig. S7).

Because the sampling strategy prioritised fish larvae, most misidentifications occurred at the larval stage within families, rather than among juveniles or adults. Within the family Channichthyidae, the most commonly misidentified species were *Pseudochaenichthys georgianus*, *Chaenocephalus aceratus* and *Chionodraco rastrospinosus*. *Ps. georgianus* was often misidentified as *Neopagetopsis ionah*, *Pagetopsis macropterus* or *Chaenodraco wilsoni*. These errors were observed exclusively in Subarea 48.2, whereas all *Ps. georgianus* samples from Subarea 48.3 were correctly identified. Notably, the misidentifications originated from observers aboard two different fishing vessels, indicating that the errors were not attributable to a single individual. However, these misidentifications were restricted to the 2023 season. For *Ps. georgianus*, misidentified samples accounted for 23.3% of the genetically confirmed Channichthyidae samples and 6.9% of the total number of samples.

In the case of *C. aceratus* and *C. rastrospinosus*, both species were misidentified as *Cryodraco antarcticus*. These errors spanned both fishing seasons and involved observers

from three different fishing vessels, accounting for 18.3% of misidentified Channichthyidae samples and 5.4% of all samples analysed. The only icefish species that was consistently correctly identified at all developmental stages was the mackerel icefish, *Champsocephalus gunnari*.

Within the family Nototheniidae, the most frequently misidentified species were *Notothenios larseni* and various *Trematomus* species. *N. larseni* accounted for 50.7% of the total Nototheniidae samples and was occasionally misidentified as *Gobionotothen gibberifrons* or *L. nudifrons*, which represented 4.2% of the total. Conversely, *Trematomus* species like *T. eulepidotus* were misidentified as *N. larseni* and *T. newnesi.* Additional misidentifications included *T. hansoni* being recorded as *G. gibberifrons*, and *T. newnesi* was misidentified as *T. eulepidotus.* All samples for *Notothenia coriiceps* and *N. rossii* were correctly identified; however, these corresponded only to juvenile and adult specimens. Larvae of the Antarctic silverfish, *Pleuragramma antarcticum,* and the Antarctic toothfish, *Dissostichus mawsoni*, were also correctly identified in all cases.

Among the Myctophidae, species of the genus *Electrona* comprised 46% of myctophid bycatch and exhibited the highest incidence of misidentifications. Specifically, 43.0% of *E. antarctica* and *E. carlsbergi* samples were misidentified, with *E. antarctica* most often misidentified as *E. carlsbergi*. In contrast, only three instances of *E. carlsbergi* were misidentified as *E. antarctica.* Additionally, *Protomyctophum bolini* was misidentified as *E. carlsbergi* on a single occasion. These identification errors occurred across both sampling years, in all three subareas, and on multiple vessels. *Gymnoscopelus nicholsi* and *Krefftichthys anderssoni* were consistently correctly identified. For *G. nicholsi,* all samples were juveniles or adults, whilst for *K. anderssoni,* all larval specimens were accurately identified. Only three adult *K. anderssoni* specimens were misidentified as *Protomyctophum* sp.

The few specimens identified only to the genus level corresponded to juveniles or adults of *Bathylagus tenuis, Lepidion ensiferus, Muraenolepis marmorata, Macrourus whitsoni, N. annulata* and *E. antarctica.* Samples that remained unidentified or classified as unknown included juveniles or adults of *Psilodraco breviceps, C. wilsoni, Antimora rostrata, Mancopsetta maculata* and *A. tricholepis* (Table 4).

Discussion

The fish bycatch associated with the Antarctic krill fishery, sampled during the present study, comprises a taxonomically diverse assemblage of 53 species across 11 families and multiple developmental stages, highlighting the value of integrative taxonomy in determining species composition in this system. The substantial discrepancies detected between morphological identifications conducted by fishery observers and genetic identifications indicate that reliance on visual identification alone underestimates bycatch diversity. Accurate characterisation of bycatch is fundamental for effective fisheries management, and these results highlight the need for a complementary application of both morphological and molecular identification approaches.

Morphological identification by trained observers remains essential for real-time monitoring and rapid assessments at sea. However, molecular tools provide critical taxonomic resolution where visual identification is limited, such as for damaged specimens, early life stages or morphologically similar taxa. Integrating these approaches enables more reliable estimates of bycatch composition and diversity, thereby improving the quality of data used to inform management decisions.

In the context of the genetic identification of the bycatch, sound phylogenetic relationships were inferred from the two mitochondrial markers, which can be summarised in three main findings:

1. Monophyly of Notothenioidei: One of the most prominent branching patterns observed was the monophyly of Notothenioidei, grouping together all the representative families of this suborder, i.e. Channichthyidae, Bathydraconidae, Harpagiferidae and Nototheniidae. Internal nodes also reflected known phylogenetic relationships among closely related families; for example, Channichthyidae species clustered closely with Bathydraconidae, consistent with their relatively recent divergence, approximately 7 million years ago (Kim et al. 2019). Within Nototheniidae, the clustering patterns likely reflect the family's substantial ecological and morphological diversification. The evolution of antifreeze glycoproteins (AFGs) and their secondary loss in some lineages contributed to phylogenetic distinctions among genera, such as *Notothenia, Trematomus* and *Dissostichus* (Fig. 2). Behavioural adaptations were also evident. For instance, *P. antarcticum*, the only truly pelagic nototheniid, was placed distinctly, reflecting its adaptation from a benthic to a pelagic lifestyle (Bargelloni et al. 1994).

2. Clustering of Myctophidae: Myctophid species formed a distinct group, though within a broader clade that included more distantly related families and showed lower support at higher taxonomic levels. Nevertheless, all myctophid species were correctly grouped, with clear separation among the closely related genera *Electrona, Krefftichthys* and *Protomyctophum,* and the monophyletic *Gymnoscopelus*. This clustering pattern is consistent with previous phylogenetic studies (Van de Putte et al. 2012, Christiansen et al. 2018, Freer et al. 2022).

3. Other families and higher-level phylogeny: Although the phylogenetic placement of several other families has been infrequently addressed in the literature (e.g. Baldwin

and Johson 1996; Doiuchi and Nakabo 2006; Roa-Varón and Ortí 2009; Radchenko 2015), coherent phylogenetic relationships emerged in this study that align with previous findings at the order level. For instance, species within Macrouridae and Moridae clustered together, forming a well-supported Gadiformes clade. Similarly, representatives of Anotopteridae, Paralepididae and Scopelarchidae were grouped within Aulopiformes, consistent with established higher-level taxonomy.

Among the genetic markers employed, the mitochondrial *cox1* gene proved effective for species-level identification. Its high interspecific variability, coupled with relatively low intraspecific divergence (Hebert et al. 2003; Ivanova et al. 2007), allowed clear discrimination among closely related taxa. The complementary use of the mitochondrial control region further enhanced taxonomic resolution, reinforcing the value of a multi-marker approach. However, in contrast to the consistent phylogenetic placement achieved with *cox1*, the control region phylogeny showed a discrepancy: the Myctophidae sample did not cluster with its expected reference sequence but instead grouped among icefish taxa. This discordance likely reflects the intrinsic properties of the control region and methodological aspects of sequencing.

When interpreting control region phylogenies, the influence of mitochondrial heteroplasmy and locus-specific sequence characteristics must be considered. Mitochondrial heteroplasmy, the coexistence of multiple mtDNA haplotypes within a single individual, is particularly common in the non-coding control region (Malik et al. 2002; Parakatselaki and Ladoukakis 2021), which exhibits high mutation rates and substantial length and sequence variation relative to coding regions. This increased intragenomic diversity, together with complex sequence features such as tandem repeats and secondary structures, can complicate the inference of consensus sequences, sequence alignment and phylogenetic inference (Satoh et al. 2016; Parakatselaki and Ladoukakis 2021). Consequently, heteroplasmic variants are frequently detected in control region datasets and tend to occur at higher frequencies than in coding regions (Wallace and Chalkia 2013). Although Oxford Nanopore long-read technology is well suited for spanning repetitive or structurally complex mitochondrial regions, its error profile remains higher on average than that of Sanger sequencing, particularly at individual base positions (Liu-Wei et al. 2024) and in low-complexity stretches (Santos et al. 2025). These characteristics can affect consensus calling when multiple haplotypes are present, as sequencing errors may overlap with true biological variation and are not always fully resolved by base-calling algorithms or post-sequencing correction approaches (Delahaye and Nicolas 2021).

In control region amplicons containing heteroplasmic variants, the combination of genuine biological variation and platform-specific base-calling ambiguity can produce consensus sequences that diverge from species reference sequences, potentially resulting in misleading phylogenetic placement, such as the clustering of a myctophid (*E. antarctica*) within an icefish clade observed here. In contrast, coding regions such as *cox1* typically exhibit lower levels of heteroplasmy and more conserved sequence evolution, and when sequenced using Sanger technology, they yield high-fidelity consensus sequences that align consistently with reference databases. Together, these factors highlight the importance of multi-marker and cross-platform validation when interpreting control region phylogenies, particularly in taxa exhibiting complex mitochondrial DNA variation.

In the present study, several measures were implemented to mitigate these issues. Single-specimen amplicon sequencing was employed to reduce the formation of chimeric amplicons by preferentially amplifying a dominant DNA molecule (Pomerantz et al. 2022). Sequencing was conducted using a kit with a reported accuracy of 99%, and base-calling was repeated during post-processing. Additional quality controls included length filtering (200–2000 bp), a quality score threshold of Q9 (corresponding to 99% expected read accuracy), and the removal of low-quality reads prior to demultiplexing. Consensus sequences were further screened based on a minimum read support threshold (n = 30), following established protocols (Erkenswick et al. 2024; Sánchez-Vendizú et al. 2025). The Myctophidae (*E. antarctica*) control region sequence with unexpected phylogenetic placement had a mean Q-score of 9.0014, was supported by 56 reads and contained two ambiguous bases (W = A/T; R = A/G).

This study employed two sequencing technologies, Sanger sequencing for *cox1* and Oxford Nanopore sequencing for the control region, which differ substantially in sequencing chemistry, read length and error profiles. Sanger sequencing is widely regarded as the benchmark for high per-base accuracy, with typical error rates below 0.1%, making it particularly well suited for short, conserved amplicons and precise phylogenetic placement (Heather and Chain 2016; Shendure et al. 2017). In contrast, Oxford Nanopore sequencing offers long-read capabilities and high resolution of complex structural variants but historically exhibits higher raw per-base error rates, particularly in homopolymeric and low-complexity regions (Delahaye and Nicolas 2021; Srivathsan et al. 2021; Liu-Wei et al. 2024). These systematic error profiles can influence consensus sequence generation and, in highly variable loci, may affect phylogenetic inference if not carefully controlled. While control region phylogenies should therefore be interpreted with caution, the remaining samples across both markers and technologies indicate that sequencing errors were generally low and unlikely to systematically bias species assignment. The isolated instance of phylogenetic discordance observed

in the control region is therefore more plausibly explained by the combined effects of locus-specific variability, mitochondrial heteroplasmy and platform-specific error profiles. Taken together, these results support the view that structurally conserved and variable loci, and Sanger and nanopore sequencing, are complementary rather than competing approaches, and that their combined use strengthens phylogenetic inference and species identification when applied with appropriate validation and quality control.

The accurate identification of species remains a crucial component in the study of natural ecosystems, supporting critical research in conservation biology, biogeography, ecology, evolutionary biology and the sustainable management of fisheries (Hiddink et al. 2008; Ward et al. 2009; Fischer 2013; Omer 2017; Singh et al. 2023). In the context of fish bycatch, precise species inventories are essential, not only for the sustainable management of natural resources by revealing the extent of fishing impacts on non-target species, but also for enhancing our current and future understanding of species distributions and life-history traits. In the krill fishery, practices for identifying fish bycatch vary both between vessels and between fishery observers and crew members responsible for bycatch reporting (CCAMLR 2024). The 25 kg subsample analysed by observers is often dominated by larval or juvenile fish, whereas vessel crew, who typically inspect the entire catch, may have difficulty detecting smaller individuals (< 10 cm in length) during processing (CCAMLR 2025b). This variability in sampling methods and bycatch handling protocols introduces substantial uncertainties into bycatch estimates, as observer samples may not reflect the full-size range or species composition of the total bycatch. Furthermore, misidentification or non-identification of non-target species compounds this problem, limiting the accuracy and ecological relevance of the data. These complicate efforts to interpret bycatch data accurately and hinder the ability to assess ecosystem impacts or inform management measures with confidence. Taken together, these findings underscore the importance of integrating molecular tools with traditional morphological identification to achieve accurate and comprehensive bycatch reporting. While onboard morphological identification remains essential for real-time monitoring and ecological context, genetic approaches provide critical resolution where visual methods are constrained. The primers and reference database developed in this study establish a robust framework for future applications, including next-generation sequencing, and support improved biodiversity assessments and ecosystem-based management of the Antarctic krill fishery.

Observer identifications

In terms of the observer's identification scores, subarea 48.2 (Southern Scotia Sea including South Orkney Islands) exhibited the highest proportion of misidentifications, accounting for nearly half of all errors recorded in the study. This was largely due to frequent misidentifications of icefish species. Notably, observers' accuracy appeared to be influenced by spatial factors, particularly in the case of *Ps. georgianus*. Identification scores for this species were significantly higher in area 48.3 compared to Subareas 48.1 and 48.2, where larval specimens were often confused with *Pagetopsis* species, *C. aceratus* and *C. wilsoni*. The distribution of *Ps. georgianus,* as opposed to *C. wilsoni* and *P. macropterus,* spans from the northern parts of the Antarctic Peninsula northward to South Georgia, encompassing all three subareas and overlapping with the ranges of the species in the southern areas. In contrast, *C. wilsoni* and *Pagetopsis,* although circum-Antarctic, are predominantly found in Subareas 48.1 and 48.2 (Ekau 1990; La Mesa et al. 2019). This spatial overlap may create a confounding spatial effect that influences observers to be more prone to misidentifying a species when the number of possible encountered species increases. While icefish species exhibit distinctive morphological features and larval pigmentation patterns (Kellermann and North 1989; Kellermann 1990), these characteristics can be subtle and difficult to distinguish among closely related species. In the case of *Ps. georgianus*, distinguishing features such as its short, deep body, large head with an elongated snout and heavily pigmented pelvic fins help differentiate it from *C. aceratus* and *C. wilsoni*, but not as easily from *Pagetopsis* species, which are more similar-looking and for which the extent and arrangement of lateral pigmentation may be more diagnostic (Kellermann and North 1989). A similar challenge was observed in the identification of the myctophids *E. carlsbergi* and *E. antarctica.* Subtle morphological traits such as head shape, the presence of a suborbital photophore and the arrangement of supra- and infra-caudal glands can aid in distinguishing *E. carlsbergi* from its congener (Gon and Heemstra 1990). However, Myctophids are difficult to identify because several identifying features are often damaged during trawling. Accurate identification is further complicated by the poor preservation of scales and light organs in collected specimens, and by the overlapping geographic ranges of these species, which span all three subareas of Area 48 (Gon and Heemstra 1990).

Another critical factor affecting the accuracy of observer identifications across sampling seasons was the ability to correctly identify specimens in transitional stages between larvae and juveniles. This was particularly evident for *N. larseni,* where specimens larger than 40 mm TL were generally identified correctly, whereas smaller specimens were

often misidentified as morphologically similar species such as *T. hansoni* and *T. eulepidotus,* or even as less closely related species such as *G. gibberifrons.* This highlights the importance of larval pigmentation patterns in similar-looking species, such as those in the families Channichthyidae and Nototheniidae, where subtle differences in pigmentation distribution and concentration aid species discrimination (Efremenko 1983).

Observers had fewer difficulties identifying species with more distinct pigmentation patterns, such as *D. mawsoni, Gymnodraco acuticeps*, and *C. gunnari,* as well as species with unique anatomical traits. For instance, larval *K. anderssoni* is characterised by an elongated body, cone-shaped eyes, and a ventral row of pigments extending along the elongated gut, features that facilitate its identification. However, specimen damage during net collection posed a significant challenge. Larval fish often lost key pigments, whilst adults, particularly myctophids, were prone to losing or damaging scales and light organs, key features for species identification in later stages. These issues, coupled with the lack of ecological information regarding species distributions, contributed to misidentifications. Based on the present results, we emphasise the need for updated identification materials that directly address these challenges. These should clearly illustrate differences in pigmentation patterns among congeneric species and how these change throughout ontogeny. Additional diagnostic features, such as body and head shapes, gut length and fin pigmentation patterns, are suggested, as they are particularly useful for improving species-level identification in the Antarctic krill fishery.

Krill associations and the implications for fish populations

Antarctic krill (*E. superba*) plays a central role in the Southern Ocean food web, serving as a primary food source for many vertebrates, including fish (Kock et al. 2012; Moreira et al. 2023). Our observations from the Antarctic krill fishery indicate that a broad range of fish species are being incidentally caught as bycatch. Although the present sample set is biassed towards larval fish, reflecting the sampling approach used by observers, who typically examined a 25 kg subsample of the catch (CCAMLR 2025b), larger juveniles and adults were occasionally recorded. However, it is important to recognise that larger fish may be removed from the catch before the observer collects their sample, either automatically (e.g. through mesh screens or water-flow separation systems) or manually during factory processing. Moreover, this reflects two key ecological considerations: first, not all bycaught species rely on krill as a food source; and second, many larvae and juveniles are likely caught incidentally as the net descends through the water before reaching the krill swarms, rather than as a result of their trophic association with krill. However, species such as *C. gunnari*, *Ps. georgianus, C. aceratus, E. antarctica, G. nicholsi* and *G. braueri* exhibit varying degrees of krill dependency as adults (Kock et al. 1994; Flores et al. 2004; Clarke et al. 2008; Main et al. 2009; Kock et al. 2012; Sanders et al. 2019; Moreira et al. 2023). For these species, the combined pressure of natural interannual fluctuations in krill abundance and incidental capture by the fishery, particularly during years of low krill abundance, may increase the risk to their populations and should be considered in the context of ecosystem-based fishery management.

The krill fishery is seasonal, with operations distributed across the subareas. Fishing typically occurs in subarea 48.2 during summer, 48.1 in autumn and 48.3 in winter. Since 2009, krill catches have increased, and fishing efforts have become more concentrated in subarea 48.2 (Thorpe et al. 2024). This concentration of fishing in a single subarea raises concerns about potential impacts on species whose larval stages are also concentrated in the same area. In our findings, the highest proportion of species misidentifications occurred in subarea 48.2, further heightening concerns for the fish species caught as bycatch in this region.

Conclusion

Spatial variability in misidentification rates among fishing areas further emphasises the importance of genetic verification. Differences in species assemblages, relative abundances and operational conditions likely contribute to uneven identification accuracy, suggesting that observer-based data alone may introduce spatial bias into bycatch estimates. Molecular identification provides a standardised means to validate and complement observer records, thereby improving the consistency and comparability of bycatch data across regions.

These findings highlight the critical importance of providing observers with user-friendly identification materials that incorporate detailed taxonomic keys, including illustrations across different life-history stages. In addition, appropriate training and equipment, such as stereomicroscopes, will further enhance accurate species identification in the field. Additionally, incorporating ecological information on the seasonal occurrence and developmental timing of species may help narrow the pool of likely taxa that observers might expect to encounter within specific subareas and timeframes. However, such ecological information must be framed with caution, in a rapidly changing environment, as historical distributions and life-history patterns may shift. As such, species distribution maps and developmental timing should be

clearly annotated as historically derived and acknowledge the potential for future ecological change. Importantly, these recommendations are not only relevant to the krill fishery but may also inform observer protocols and bycatch monitoring strategies in other fisheries operating in Area 48, such as the toothfish longline and icefish fisheries, and beyond. As ecosystems worldwide face similar challenges due to climate change and increased fishing pressure, the adoption of standardised, ecologically informed identification tools and observer support systems can enhance data quality and improve the reliability of bycatch assessments across a range of fisheries and regions.

The ever-pressing issue of reference sequences available in open-access platforms was considered throughout this study. To address this, we have contributed to expanding the molecular reference database for Southern Ocean fishes by developing and validating genetic tools that effectively captured a broad taxonomic range. These results provide a robust reference library (see BioProject PRJNA1270765 and Romero Martínez et al. 2025) for fish species within CCAMLR Area 48 and lay the groundwork for future applications of high-throughput sequencing (HTS) approaches. Such tools can facilitate comprehensive assessments of the fish diversity associated with the krill fishery, extending beyond bycatch to include all co-occurring species. Ultimately, this work supports the development of standardised, accessible identification resources and strengthens the accuracy of bycatch reporting across CCAMLR- managed fisheries.

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Data availability Data supporting this study have been submitted to the British Antarctic Survey -Polar Data Centre; all associated files will be available to the general public following a one-month embargo. The dataset is due to be released on June 30 th, 2025, at https://doi.org/10.5285/9c459656-5fe4-44f7-860f-da287111016c. A physical DNA bank was established for the project's tissue and genomic DNA samples and can be found as part of the biological archives at BAS under the logistic case number 22903. Adult specimens were deposited in the Natural History Museum, London, under the specimen numbers 2024.7.1.17 and 2026.2.1.1–2026.2.1.29. Genetic data for *cox1* and control region are available from GenBank under BioProject PRJNA1270765 with accession numbers PQ686535-45, PQ727374-PQ736688, PQ728912-86, PQ736524-PQ736688, PQ742065-PQ742162, and PQ672629-PQ672777 (due to be released on June 30 th, 2025).

Declarations

Conflict of interest The authors declare no competing interests.

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