Received: 15 July 2025 | Revised: 3 June 2026 | Accepted: 2 July 2026

DOI: 10.1111/jfb.70577

JOURNAL OF FISH BIOLOGY fsbi

BRIEF COMMUNICATION

DNA barcoding reveals the presence of Whitson's grenadier, *Macrourus whitsoni*, in sub-Antarctic waters of South Georgia, Southern Ocean

M. L. Romero Martínez[1] | J. Abreu[1,2] | J. P. Queirós[1,2] | J. C. Xavier[1,3] | P. R. Hollyman[1,4] | E. Fitzcharles[1] | M. A. Collins[1]

[1]British Antarctic Survey, NERC, Cambridge, UK

[2]MARE-Marine and Environmental Sciences Centre/ARNET-Aquatic Research Network, Department of life Sciences, University of Coimbra, Coimbra, Portugal

[3]Associate Laboratory TERRA, Department of Life Sciences, Centre for Functional Ecology – Science for People & the Planet (CFE), Coimbra, Portugal

[4]School of Ocean Sciences, Bangor University, Menai Bridge, UK

Correspondence
M. L. Romero Martínez, British Antarctic Survey, NERC, High Cross, Madingley Road, Cambridge CB3 0ET, UK.
Email: mamero@bas.ac.uk

Present address
J. P. Queirós, CIIMAR/CIMAR LA, Interdisciplinary Centre of Marine and Environmental Research, University of Porto, Terminal de Cruzeiros do Porto de Leixões, Matosinhos, Portugal.

Funding information
Universidade de Coimbra, Grant/Award Numbers: SFRH/BD/144320/2019, 2020.07291.BD; MARE, Grant/Award Numbers: UIDB/04292/2020, UIDP/04292/2020; Associate Laboratory ARNET, Grant/Award Number: LA/P/0069/2020; Centre for Functional Ecology – Science for the People & the Planet, Grant/Award Number: UIDP/04004/2025

Abstract

Macrourid species constitute the main bycatch in Southern Ocean toothfish longline fisheries. We report the first confirmed record of Whitson's grenadier, *Macrourus whitsoni*, in the South Georgia toothfish fishery. Mitochondrial *cox1* DNA barcoding confirmed its presence in bycatch samples collected around South Georgia and the northern South Sandwich Islands, with approximately 1% divergence from its congener, *M. caml*. Haplotype network analysis revealed a single dominant haplotype and two peripheral haplotypes, indicating a well-connected Southern Ocean stock. These findings highlight the need for accurate species-level identification to inform effective fisheries management.

KEYWORDS

cox1, fisheries, *macrourus*, management, Southern Ocean

The family Macrouridae, commonly known as grenadiers or rattails, comprises 375 of the 629 species in the order Gadiformes and is globally distributed from the upper continental slopes to the abyss, ranging from 500 m to over 5000 m deep (Cohen et al., 1990; Fricke & Fong, 2026; Iwamoto, 2008). While a few species, such as *Macrourus berglax* and *Coryphaenoides rupestris*, are targeted in commercial fisheries in the North Atlantic, many other macrourids are caught as bycatch (Atkinson, 1995).

The genus *Macrourus* comprises five morphologically similar species, *Macrourus caml* McMillan et al., 2012, *M. carinatus* (Günther 1878), *M. holotrachys* Günther (1878), *M. whitsoni* (Regan 1913) and *M. berglax* Lacepède (1801), with the first four species occurring in the Southern Ocean (Cohen et al., 1990; Gon et al., 2021). Prior to the description of *M. caml* in 2012 (McMillan et al., 2012), only three *Macrourus* species were recognised in the Southern Ocean (Gon & Heemstra, 1990). *M. whitsoni* was considered to have the widest distribution, occurring from the Antarctic continent to sub-Antarctic islands such as the South Sandwich Islands, Heard Island and McDonald Islands (Dell et al., 2015; Hollyman et al., 2022; Iwamoto, 1990). McMillan et al. (2012) described *M. caml* from specimens collected in the Ross Sea that had initially been identified as *M. whitsoni*, noting that many specimens previously attributed to *M. whitsoni* and *M. carinatus* were likely *M. caml*. Smith et al. (2012) confirmed the genetic identity of *M. caml* through DNA barcoding of samples from eight locations across the Southern Ocean. More recently, Gon et al. (2021) reported on the distribution of Southern Ocean *Macrourus*, suggesting that *M. whitsoni* was confined to Antarctic waters.

South Georgia and Shag Rocks (Atlantic sector of the Southern Ocean) are surrounded by highly productive waters that support a diverse, depth-stratified fish assemblage (Gregory et al., 2017). Among deep-sea fishes, macrourids dominate at depths greater than 600 m (Gregory et al., 2017). Three *Macrourus* species reported from a deep-water trawl survey at South Georgia in 2003 were assumed to be *M. holotrachys*, *M. carinatus* and *M. whitsoni* (Belchier et al., 2003). Following the description of *M. caml*, Fitzcharles (2012, 2014) sequenced the mitochondrial Cytochrome c oxidase subunit I (*cox1*) and 16S ribosomal RNA (16S rRNA) genes from *Macrourus* specimens caught during the 2003 survey and from fisheries in South Georgia and the South Sandwich Islands. Fitzcharles (2014) identified four distinct species clusters, three of which were from South Georgia and corroborated the presence of *M. whitsoni* in the South Sandwich Islands. The three species confirmed at South Georgia were *M. holotrachys*, *M. carinatus* and *M. caml*. Since then, it has been assumed that *M. whitsoni* is a more southerly species and does not occur at South Georgia (Andrews & Sharov, 2024; Gregory et al., 2017). However, a recent analysis of the distribution and ecology of four *Macrourus* species caught as bycatch in the toothfish longline fishery at South Georgia (Abreu et al., 2026) reported specimens identified as *M. whitsoni* based on morphometric characters (Table S1), therefore requiring more precise species identification.

In the Southern Ocean, macrourids represent a key prey group for both Patagonian (*Dissostichus eleginoides*) and Antarctic (*Dissostichus mawsoni*) toothfish (Queirós et al., 2024; Roberts et al., 2011; Stevens et al., 2014) and constitute the main component of bycatch in fisheries targeting toothfish (Collins et al., 2010; Laptikhovsky, 2005; Pinkerton et al., 2013). Thus, accurate knowledge of the distribution of macrourid species is crucial for the effective management of these longline fisheries. Furthermore, the specimens reported by Abreu et al. (2026), identified as *M. whitsoni* in the northeastern and eastern areas of South Georgia, and showing a clear preference for depths over 1500 m, require genetic analysis to verify the species records from South Georgia.

Ecosystem-based fisheries management, such as that implemented by the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) (Constable, 2002), relies on a comprehensive understanding of the biology and ecology of target species, as well as those occurring in sympatry that are regularly caught as bycatch. Hence, it is important to accurately identify bycatch species. To clarify the presence of *M. whitsoni* in South Georgia waters, we conducted a DNA barcoding analysis to explore genetic partitioning among members of the *Macrourus* genus in the Southern Ocean and the relative placement of specimens morphologically identified as *M. whitsoni* by Abreu et al. (2026).

Putative *Macrourus whitsoni* specimens were collected during the toothfish fishing seasons in South Georgia (CCAMLR Subarea 48.3) from 2021 to 2023 (May–August) and in the South Sandwich Islands (CCAMLR Subarea 48.4) in 2020 (March–April) (Figure 1). Samples were collected by researchers and fishery observers at depths of 800–1800 m, within the operational range (700–2250 m) permitted under CCAMLR conservation measures (41–02[1] & 41–03). Species-level identifications followed the CCAMLR bycatch identification guide (CCAMLR, 2019) and the criteria outlined in Table S1. Subsequent verification of taxonomic identification was performed by the research team onboard the fishing vessel or at King Edward Point Research Station, South Georgia. Following identification, muscle tissue from 42 samples was excised from the lateral body region and preserved at −20°C until further analysis.

Genomic DNA (gDNA) was extracted from 25 mg of muscle tissue per specimen using the DNeasy® Blood and Tissue Kit (Qiagen Ltd., West Sussex, UK), following the manufacturer's instructions. The extracted gDNA was eluted in 50 μL of elution buffer. A 643-bp fragment of the *cox1* gene was amplified with group-specific primers developed by Romero Martínez et al. (2026). Each 15-μL PCR reaction contained 5.9 μL of ultrapure water, 7.5 μL of 2× MyTaq HS Master Mix (Meridian Bioscience, Bioline Reagents Ltd., UK), 0.3 μM of each primer and 1 μL of DNA template. Thermocycling conditions followed those of Romero Martínez et al. (2026). PCR products were visualised by gel electrophoresis, purified with ExoSAP-IT Express (Applied Biosystems, Thermo Fisher Scientific, Santa Clara, CA, USA), and Sanger-sequenced at Eurofins Genomics UK (Wolverhampton, UK).

[1]Although Conservation Measure 41–02 has not been in force since 2021, its provisions have continued to be adhered to in practice. For current and historical measures, see the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), "Conservation Measures" https://www.ccamlr.org/en/conservation-and-management/conservation-measures.

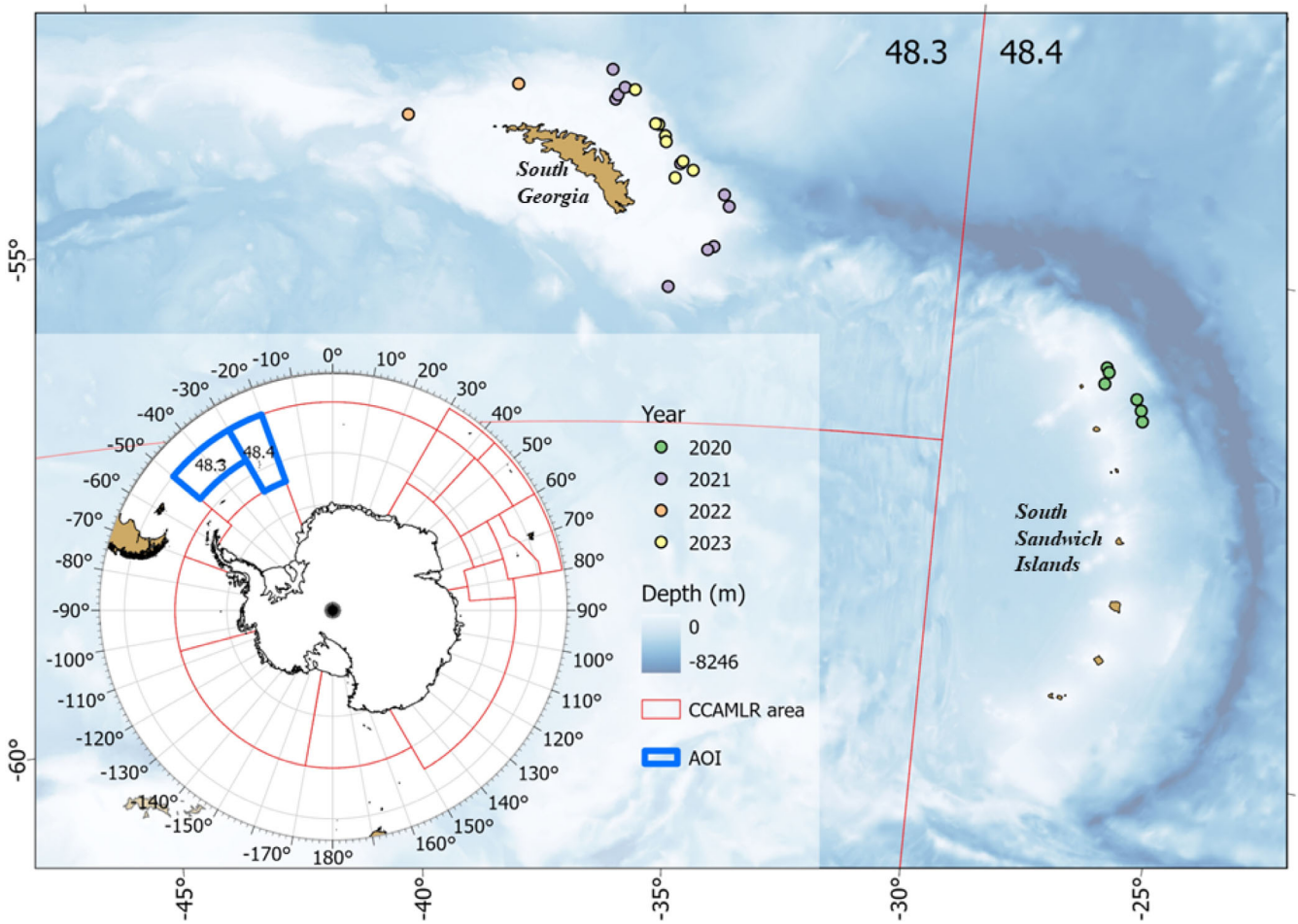

FIGURE 1 Sampling sites in South Georgia (Subarea 48.3) and the northern South Sandwich Islands (Subarea 48.4). See Gon et al. (2021) for the current distribution of confirmed *M. whitsoni* in the Southern Ocean. See Abreu et al. (2026) for an updated synthesis of the current *macrourid* species occurrence in South Georgia (Subarea 48.3).

Sequenced data were processed in Geneious Prime v.2025.0.3 (GraphPad Software LLC) to inspect electropherograms for base quality scores, trim primers and assemble contigs using the 'De novo' function. Reference sequences for *M. caml*, *M. carinatus*, *M. holotrachys* and *M. whitsoni* were obtained from the Barcode of Life Database (BOLD), including those published by Smith et al. (2012) and Gon et al. (2021), and unpublished sequences for *M. caml* and *M. whitsoni* from Fitzcharles (2014). Sequences for *M. whitsoni* identified on BOLD before 2012 were treated as unidentified to verify their identity. Curated sequences for Abreu et al. (2026) samples and Fitzcharles (2014) were submitted to GenBank under accession numbers PV490009-PV490044; PV618429-PV618434 and PV697571-PV697600, respectively.

Maximum-likelihood reconstruction of phylogenetic relationships was performed in MEGA v12 (Kumar et al., 2024), using the T92 + I model with a fraction of sites allowed to be evolutionarily invariant (Tamura, 1992), and 1000 bootstrap replicates. The most suitable nucleotide substitution model was selected using JModelTest v2.1.10 (Darriba et al., 2012; Guindon & Gascuel, 2003) based on Akaike's information criterion corrected for small sample sizes (AICc) and the Bayesian information criterion (BIC). Within- and between-group distances (uncorrected P and composite likelihood) were estimated using MEGA v12 (Kumar et al., 2024). Significant differences between pairwise distances were tested by PERMANOVA in R using the '*vegan*' package (Oksanen et al., 2025; R Core Team, 2025). Three outgroups from the order Gadiformes were included: *Coryphaenoides rupestris* (GenBank ID: KJ128468), *C. striaturus* (KX656427) and *Muraenolepis marmorata* (EU326378). Bayesian phylogenetic analyses were performed with Beast v10.5.0 and related programmes BEAUti and TreeAnnotator (Suchard et al., 2018). A Monte Carlo simulation was run for 1×10^7 generations, saving the current tree every 1000 generations. A consensus maximum clade credibility tree was created with a burn-in of 1000.

Summary statistics for *M. whitsoni* populations were calculated using DNAsp v5 (Librado & Rozas, 2009). Significant levels for estimates of within-populations genetic variation (Tajima's D, R_2 and Fu & Li's FS and D) were assessed using coalescent simulations with 5000 replicates. The haplotype network was constructed using the TCS statistical parsimony method in PopART (Clement et al., 2002).

The estimated pairwise distances between sequences are shown in Table S2. Within-species sequence divergence ranged from 0.00% to 0.32% (Table 1), with *M. carinatus* having the highest value (0.32%), most likely reflecting the number of BINs (2) determined by BOLD (BINs are Barcode Index Numbers assigned to specimens with sequences of sufficient quality and determined by established species delimitation methods); all the other *Macrourus* species formed one BIN per species. By contrast, *M. caml*, *M. whitsoni* and the Abreu et al. (2026) samples were at the lower end of the within-species divergence. Pairwise distances between species ranged from 0.00% to 1.93% as calculated by the two pairwise distance approaches. The greatest divergence (1.93%) occurred between *M. carinatus* and *M. caml*. For the samples morphologically identified as *M. whitsoni* by Abreu et al. (2026), interspecific distances from *M. whitsoni* were the lowest (0.00%); followed by 0.64 and 0.65% between these samples and both *M. holotrachys* and *M. caml*, and 1.71% divergence from *M. carinatus*. The PERMANOVA based on the pairwise genetic distances showed significant differences between *M. caml* and the Abreu et al. (2026) samples ($F = 482.4$, $R^2 = 0.95$, $p = 0.001$), indicating that 95% of the genetic variation was explained by species identity and suggesting strong genetic differentiation between the two. By contrast, comparisons between *M. whitsoni* and the Abreu et al. (2026) samples were not significant ($F = -3.85$, $R^2 = -0.14$, $p = 1.00$).

The phylogenetic reconstruction showed strong support for the monophyly of the group (Figure 2; see Figure S1 for the full-length tree showing the phylogenetic placement of Abreu et al.'s samples).

TABLE 1 Pairwise distances between *Macrourus* species. Values below the diagonal are uncorrected-p distances, and those above are composite likelihood distances. The mean within-group uncorrected-p distances are shown in blue. For Abreu et al. (2026), samples from South Georgia (SG) and the South Sandwich Islands (SS).

	Abreu SG	Abreu SS	*M. whitsoni*	*M. caml*	*M. carinatus*	*M. holotrachys*	Outgroup 1	Outgroup 2
Abreu SG	0.0001	0.0000	0.0000	0.0065	0.0174	0.0065	0.2289	0.2574
Abreu SS	0.0000	0.0000	0.0000	0.0065	0.0174	0.0065	0.2287	0.2571
M. whitsoni	0.0000	0.0000	0.0005	0.0065	0.0171	0.0064	0.2289	0.1866
M. caml	0.0065	0.0065	0.0065	0.0012	0.0193	0.0087	0.2316	0.1930
M. carinatus	0.0171	0.0171	0.0174	0.0197	0.0032	0.0193	0.2207	0.1890
M. holotrachys	0.0064	0.0064	0.0065	0.0087	0.0190	0.0021	0.2240	0.1929
Outgroup 1	0.1771	0.1770	0.1771	0.1794	0.1720	0.1740	0.15548	0.2013
Outgroup 2	0.1866	0.1865	0.2574	0.2682	0.2619	0.2681	0.2787	n/a

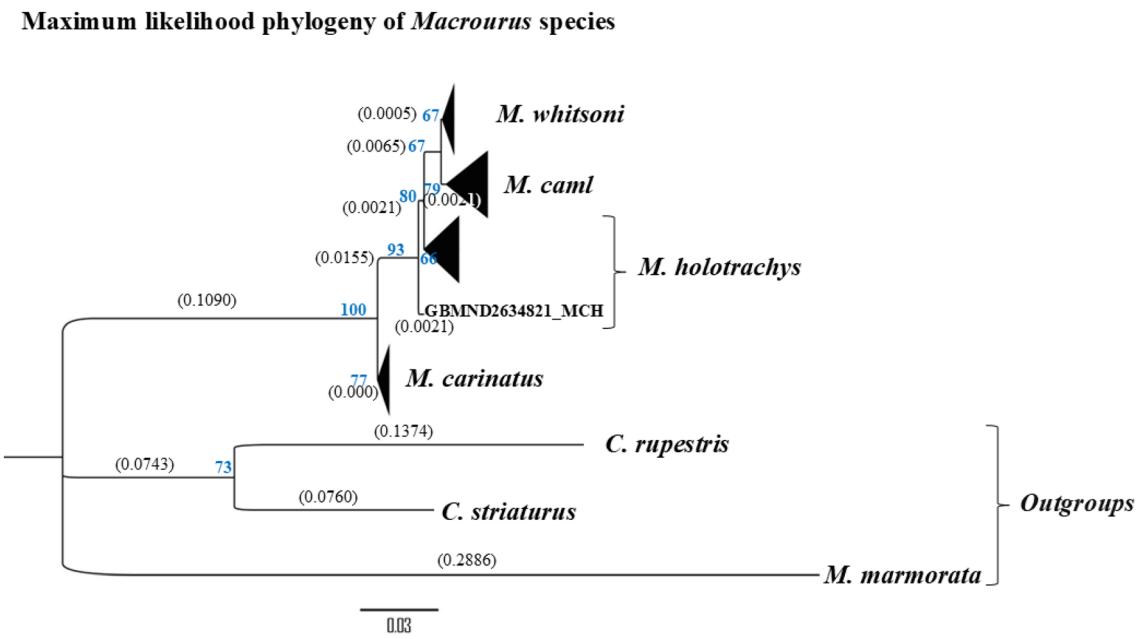

FIGURE 2 Maximum-likelihood phylogenetic relationships of partial *cox*1 sequences from Southern Ocean *Macrourus* specimens. Collapsed tree with bootstrap support given at nodes following 1000 replicates and branch lengths in brackets. Triangles denote collapsed clades, where height (vertical side to the right) is proportional to sample size and depth (to the angle joining the phylogeny) is proportional to within-clade diversity. The analysis comprised 202 sequences with 477 positions. The scale bar (0.03) represents pairwise genetic distances. Outgroups were *C. rupestris* (GenBank ID: KJ128468), *C. striaturus* (KX656427) and *M. marmorata* (EU326378).

Four clusters were clearly separated, corresponding to the four *Macrourus* species. Branch support for the individual clusters ranged from 66% to 100% in the maximum-likelihood reconstruction. The samples morphologically identified as *M. whitsoni* by Abreu et al. (2026) clustered with *M. whitsoni* reference sequences from the Ross Sea and Indian Ocean Sectors, with no distinction between samples from South Georgia or the South Sandwich Islands. Short branches separating the clusters reflect low genetic divergence among the four species. Deep internal nodes reflect the evolutionary history of Gadiformes, with *Macrourus* species and the two *Coryphaenoides* outgroups closer to each other than to the third outgroup, *M. marmorata*. The latter belongs to the suborder Gadoidei, whereas the former belongs to the suborder Macrouridae. The Bayesian reconstruction was consistent with the clustering pattern inferred under maximum likelihood. The Bayesian phylogeny recovered four clades with posterior probabilities ranging from 0.77 to 0.98 (Figure S2).

Overall, three haplotypes and three segregating sites were observed in the TCS network of *M. whitsoni* (Figure S3 and Table S3), consistent with estimates of genetic diversity between populations. The most common haplotype, *Hap1* (AAC), was shared by 75 individuals; the second most common, *Hap2* (GGT), by 4 individuals, with one from Dumont d' Urville and three from South Georgia. *Hap3* (GAC) was detected in a single individual from the South Sandwich Islands. Haplotypes were connected by 1–2 mutational steps. Haplotype and nucleotide diversity (average Hd: 0.462; π: 0.0018) were highest in the Ross Sea, followed by the Indian Ocean Sector and South Georgia within Area 48.

Summary statistics describe the pattern of sequence divergence between populations of *M. whitsoni*. Haplotype diversity (Hd: 0.120) and nucleotide diversity (π: 0.001) indicated low polymorphism, consistent with Goodall-Copestake et al. (2012). Among the five populations investigated, the South Sandwich Islands and South Georgia had the lowest values for both estimates, Hd: 0.100, π: 0.0002 and Hd: 0.175, π: 0.001, respectively. Ross Sea samples had the highest values for both estimates, followed by the Indian Ocean sector, which had intermediate values. No significant differences in neutrality estimates were observed across all but one population. In the South Sandwich Islands, Fu & Li's D statistic was significant. Negative D values reflect an excess of singletons, which may indicate purifying selection or population expansion. However, these measures of genetic variation must be interpreted collectively; whilst the values of DT, R_2 and Fs were negative or close to zero, these did not refute neutrality. Overall, the estimates of polymorphism (Tajima's D) and population growth (R_2 and Fs) were not significant and fell within expected levels that do not infringe the neutral model of evolution within populations. However, negative values and those close to zero may indicate low-frequency polymorphisms and an overrepresentation of a few haplotypes, as observed in the TCS network, thereby supporting low genetic structuring across the sampled regions.

Accurate identification of exploited fish species, both targeted and bycatch, is fundamental to the sustainable management of fisheries (Fischer, 2013; Hiddink et al., 2008; Singh et al., 2023). Misidentification of specimens can hinder the detection of population declines and obscure the impact of fishing on vulnerable or nontarget species. In the context of fish bycatch, precise species-level data are essential for evaluating ecosystem impacts and for developing mitigation strategies that minimise harm to biodiversity and promote ecosystem-based management. Therefore, developing reliable identification tools for bycatch species is critical for effective fisheries management (FAO, 2013).

As noted by Gon et al. (2021), the distributions of *M. whitsoni* and *M. caml* are only partially understood, and further studies are needed to fully characterise the circum-global distribution of *Macrourus* species in the Southern Ocean. More recently, Abreu et al. (2026) synthesised the current occurrence data of *Macrourus* species around South Georgia. In this study, we contribute to this ongoing research by providing robust confirmation of the occurrence of *Macrourus whitsoni* in the waters surrounding South Georgia and the northern South Sandwich Islands, indicating South Georgia as the new northernmost limit of *M. whitsoni*, at least in the Atlantic sector of the Southern Ocean. Moreover, the *M. whitsoni* population at South Georgia exhibits characteristics of a range-edge population, that is, smaller individuals than those in southern regions (including the South Sandwich Islands), mostly immature, and at low abundances (although low catch rates may reflect hook-size selection) (Abreu et al., 2026; Gaston, 2009).

The Macrourus phylogeny, as shown in Figure 2, shows low sequence divergence among species, consistent with previous reports by Smith et al. (2012). Although cryptic diversity has been reported at low sequence divergence (0.5%) in Southern Ocean fish (Smith et al., 2008), it is generally reflected in deep divergences among haplotypes within nominal species. Such a pattern was not evident in our results. However, the placement of the reference sequence of *M. holotrachys* (GBMND2634821) on a separate branch, distinct from the main *M. holotrachys* cluster, suggests higher genetic differentiation within this species. Overall, considerable genetic disparity was not observed among *Macrourus* species. Moreover, for *M. whitsoni*, the haplotype network analysis and genetic diversity indices indicate low polymorphism within the sampled populations, consistent with the presence of a dominant, widespread haplotype shared across all localities, together with two closely linked peripheral haplotypes separated by one and two mutational steps, respectively. This star-like pattern of low polymorphism is often indicative of high connectivity that limits the accumulation of regional mutations, recent population expansion or a genetic bottleneck (Goodall-Copestake et al., 2012). Similar results have been observed in other Gadiformes of the genus *Muraenolepis* (Fitzcharles, 2014), in the Antarctic toothfish (*Dissostichus mawsoni*) (Choi et al., 2021) and in other Antarctic fish species: *Trematomus nicolai* (Kuhn et al., 2009) and *Harpagifer bispinis* (Segovia et al., 2022), indicating that low polymorphism, due to unrestricted gene flow, reflects a shallow evolutionary history. More importantly, *M. whitsoni* has shown a preference for deeper waters compared with its congeners (Abreu et al., 2026; Gon et al., 2021; Pinkerton et al., 2013). The eurybathic nature of macrourid species, coupled with the relatively homogeneous environment of the continental slope, provides favourable conditions for these species to extend their range (Amsler et al., 2016; Gregory et al., 2017). The present results suggest

high migration rates between populations of *M. whitsoni*, with important implications for future management of the toothfish fishery. Management provisions should recognise four rather than three species, and for *M. whitsoni*, the well-connected populations across its range appear to constitute a single, large genetic stock. However, even such a well-connected stock could still be vulnerable to local collapses if mortality is high or recruitment is low.

While we acknowledge the limitations of using a single genetic marker, the evolutionary signal from the mitochondrial gene *cox*1 is robust, is well represented in reference databases and has been extensively used for genetic identification of fish (Choi et al., 2021; Christiansen et al., 2018; Fitzcharles, 2014; Gon et al., 2021; Romero Martínez et al., 2026; Smith et al., 2012) and other taxa (e.g., Sanders et al., 2025) in the Southern Ocean. In this study, this marker was well suited for identifying *Macrourus* species and for confirming the identification of our specimens. Moreover, exploration of genetic variation within the genus revealed approximately 1%–2% genetic differentiation between species, about three times higher than the within-species divergence. Nevertheless, incorporating multimarker and genomic approaches would enhance phylogenetic resolution and robustness, while more targeted approaches, such as restriction site-associated DNA sequencing (RAD-seq), could be used to examine genetic differentiation between populations. Here, we briefly explored the haplotype diversity and population-level estimates of *M. whitsoni* across locations in the Southern Ocean. Follow-up work employing the aforementioned techniques would further clarify the genetic distinctiveness within the *Macrourus* genus.

Genetic studies have revealed the extent of genetic variation and have accurately identified *Macrourus* species (Fitzcharles, 2012, 2014; Smith et al., 2012; this study). However, fishermen and fisheries observers need reliable morphological characters to distinguish species. Various morphological characters have been suggested to aid identification, including the number of rays in the pelvic fins; the number of rows of teeth in the lower jaw (McMillan et al., 2012); differences in intestinal length and the number of pyloric caeca; and the number of scales from the base of the dorsal fin to the anus (Pinkerton et al., 2013). However, it is important to note that hooks can damage the jaws, and preference should be given to the other characteristics. See Table S2 for morphological and meristic characters aiding identification of the four *Macrourus* species.

Macrouridae comprise a large part of the bycatch in longline fisheries for Patagonian toothfish (Collins et al., 2010; Gregory et al., 2017; Laptikhovsky, 2005) and Antarctic toothfish (McMillan et al., 2012; Pinkerton et al., 2013). While the current management of the longline toothfish fishery around South Georgia considers three *Macrourus* species (*M. holotrachys*, *M. caml* and *M. carinatus*) as bycatch (Andrews & Sharov, 2024), our results demonstrate the presence of all four Southern Hemisphere species in bycatch.

AUTHOR CONTRIBUTIONS

Conceptualization: M.L.R.M., J.A., M.A.C. Methodology: M.L.R.M., J.A. Validation: M.A.C., J. X.C., P.R. H. Formal Analysis: M.L.R.M. Investigation: M.L.R.M., J.A., E.F. Resources: J.A., J.Q., E.F. Data Curation: M.L.R.M. Writing—Original draft: M.L.R.M. Writing-Review & Editing: M.L.R.M., M.A. C., J.A., J.Q., J.X.C., P.R.H., E.F. Visualisation: M.L.R.M., P.R.H. Supervision: M.A.C., J.X.C. Funding Acquisition: M.A.C., J.X.C.

ACKNOWLEDGEMENTS

This work had the support of FCT through PhD Scholarships (SFRH/BD/144320/2019 and 2020.07291.BD), national funds granted to MARE (UIDB/04292/2020 and UIDP/04292/2020) and to Associate Laboratory ARNET (LA/P/0069/2020), by the Project UIDP/04004/2025 – Centre for Functional Ecology – Science for the People & the Planet and by the Portuguese Polar Program (PROPOLAR).

ORCID

M. L. Romero Martínez https://orcid.org/0000-0002-7608-9529
J. Abreu https://orcid.org/0000-0003-3424-3011
J. P. Queirós https://orcid.org/0000-0003-2763-2529
J. C. Xavier https://orcid.org/0000-0002-9621-6660
P. R. Hollyman https://orcid.org/0000-0003-2665-5075
M. A. Collins https://orcid.org/0000-0001-7132-8650

REFERENCES

Abreu, J., Hollyman, P. R., Freer, J. J., Martínez, M. L. R., Queiros, J. P., Jones, T., Phillips, R. A., Xavier, J. C., & Collins, M. A. (2026). Distribution and ecology of the four *Macrourus* species by-caught in the longline fishery at South Georgia, Southern Ocean. *Journal of Fish Biology*, 1–19. https://doi.org/10.1111/jfb.70425

Amsler, M. O., Eastman, J. T., Smith, K. E., McClintock, J. B., Hanumant, S., Thatje, S., & Aronson, R. B. (2016). Zonation of demersal fishes off Anvers Island, western Antarctic peninsula. *Antarctic Science*, *28*, 44–50. https://doi.org/10.1017/S0954102015000462

Andrews, J., & Sharov, A. (2024). South Georgia patagonian toothfish longline public certification report, in marine stewardship council fisheries assessment. Assessments South Georgia Patagonian toothfish longline – MSC Fisheries.

Atkinson, D. B. (1995). The biology and fishery of roundnose grenadier (*Coryphaenoides rupesis*; Gunnerus, 1765) in the northwest Atlantic. In A. G. Hopper (Ed.), *Deep-water fisheries of the North Atlantic slope* (pp. 51–111). Kluwer Academic Publishers.

Belchier, M., Collins, M. A., Endicott, M., Everson, I., Hawkins, S., Marlow, T., Mulvey, T., & Paterson, R. (2003). Toothfish, Skate and Longline Bycatch Survey in Subarea 48.3. CCAML WG-FSA-03/15.

CCAMLR. (2019). *Common by-catch species in CCAMLR longline and trawl fisheries*. CCAMLR. Retrieved May 25, 2025, from https://www.ccamlr.org/en/document/science/common-catch-species-ccamlr-longline-and-trawl-fisheries

Choi, H. K., Jang, J. E., Byeon, S. Y., Kim, Y. R., Maschette, D., Chung, S., Choi, S. G., Kim, H. W., & Lee, H. J. (2021). Genetic diversity and population structure of the Antarctic toothfish, *Dissostichus mawsoni*, using mitochondrial and microsatellite DNA markers. *Frontiers in Marine Science*, *8*, 666417. https://doi.org/10.3389/fmars.2021.666417

Christiansen, H., Dettai, A., Heindler, F. M., Collins, M. A., Duhamel, G., Hautecoeur, M., Volckaert, F. A. M., & Van de Putte, A. P. (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

Clement, M., Snell, Q., Walker, P., Posada, D., & Crandall, K. (2002). TCS: Estimating gene genealogies. Parallel and Distributed Processing

Symposium, International Proceedings, 2, 184. https://doi.org/10.1109/IPDPS.2002.1016585

Cohen, D. M., Inada, T., Iwamoto, T., & Scialabba, N. (1990). FAO species catalogue. Gadiform fishes of the world (order Gadiformes). FAO *Fisheries Synopsis* 125. Vol 10.

Collins, M. A., Brickle, P., Brown, J., & Belchier, M. (2010). The Patagonian toothfish: Biology, ecology and fishery. *Advances in Marine Biology*, *58*, 227–300. https://doi.org/10.1016/B978-0-12-381015-1.00004-6

Constable, A. J. (2002). CCAMLR ecosystem monitoring and management: Future work. *CCAMLR Science*, *9*, 233–253.

Darriba, D., Taboada, G. L., Doallo, R., & Posada, D. (2012). jModelTest2: More models, new heuristics and parallel computing. *Nature Methods*, *9*, 772. https://doi.org/10.1038/nmeth.2109

Dell, J., Maschetter, D., Woodcok, E., & Welsford, D. (2015). Biology, population dynamics and preliminary assessment of the long-term yield of Macrourus caml by-caught by the Australian fishery at Heard Island and the McDonald Islands (CCAMLR Division 58.5.2). CCAMLR Working Group on Fish Stock Assessment. WG-FSA-15/63.

FAO. (2013). Fish identification tools for biodiversity and fisheries assessments. In J. Fischer (Ed.), *in FAO Fisheries and Aquaculture Technical Paper No. 585*. Food and Agriculture Organization of the United Nations.

Fischer, J. (2013). Fish identification tools for biodiversity and fisheries assessments, review and guidance for decision-makers. In *FAO Fisheries and Aquaculture Technical Paper No. 585* (p. 107). FAO.

Fitzcharles, E. M. (2012). Rapid discrimination between four Antarctic fish species, genus *Macrourus*, using HRM analysis. *Fisheries Research*, *127-128*, 166–170. https://doi.org/10.1016/j.fishres.2012.02.002

Fitzcharles, E. M. (2014). Chapter 4: The phylogenetics and phylogeography of the genus *Macrourus* in Genetic Diversity of Antarctic Fish (Doctoral thesis, University of St Andrews, UK).

Fricke, R., & Fong, J. D. (2026). Eschmeyer's catalogue of fishes. Retrieved February 2, 2026, from http://researcharchive.calacademy.org/research/ichthyology/catalog/SpeciesByFamily.asp

Gaston, K. J. (2009). Geographic range limits: Achieving synthesis. *Proceedings of the Royal Society of London B: Biological Sciences*, *276*, 1395–1406. https://doi.org/10.1098/rspb.2008.1480

Gon, O., & Heemstra, P. C. (1990). *Fishes of the Southern Ocean* (p. 462). J.L.B. Smith Institute of Ichthyology. pp. 12 pls.

Gon, O., Miya, T., McMillan, P., & Leslie, R. (2021). The distribution of four species of the genus *Macrourus* (Gadiformes: Macrouridae) from the Southern Ocean based on samples from the toothfish longline fishery. *Zootaxa*, *4903*, 105–116. https://doi.org/10.11646/zootaxa.4903.1.6

Goodall-Copestake, W. P., Tarling, G. A., & Murphy, E. J. (2012). On the comparison of population-level estimates of haplotype and nucleotide diversity: A case study using the gene cox1 in animals. *Molecular Ecology Resources*, *12*, 975–984. https://doi.org/10.1111/1755-0998.12014

Gregory, S., Collins, M. A., & Belchier, M. (2017). Demersal fish communities of the shelf and slope of South Georgia and shag rocks (Southern Ocean). *Polar Biology*, *40*, 107–121. https://doi.org/10.1007/s00300-016-1929-7

Guindon, S., & Gascuel, O. (2003). A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology*, *52*, 696–704. https://doi.org/10.1080/10635150390235520

Hiddink, J. G., MacKenzie, B. R., Rijnsdorp, A., Dulvy, N. K., Nielsen, E. E., Bekkevold, D., Heino, M., Lorance, P., & Ojaveer, H. (2008). Importance of fish biodiversity for the management of fisheries and ecosystems. *Fisheries Research*, *90*, 6–8. https://doi.org/10.1016/j.fishres.2007.11.025

Hollyman, P. R., Soeffker, M., Roberts, J., Hogg, O. T., Laptikhovsky, V. V., Queirós, J. P., Darby, C., Belchier, M., & Collins, M. A. (2022). Bioregionalization of the South Sandwich Islands through community analysis of bathyal fish and invertebrate assemblages using fishery derived data. *Deep Sea Research Partt II: Topical Studies in Oceanography*, *198*, 105054. https://doi.org/10.1016/j.dsr2.2022.105054

Iwamoto, T. (1990). Macrouridae pp. 192-206. In O. Gon & P. C. Heemstra (Eds.), *Fishes of the Southern Ocean* (p. 462). J.L.B. Smith Institute of Ichthyology.

Iwamoto, T. (2008). A brief taxonomic history of grenadiers. Grenadiers of the World Oceans: Biology, stock assessment, and fisheries, Am. Fish. Soc. Symp. 63, Orlov, A. and Iwamoto, T., Eds., Bethesda: American Fisheries Society, pp. 3–13.

Kuhn, K. L., Near, T. J., Jones, C. D., & Eastman, J. T. (2009). Aspects of the biology and population genetics of the Antarctic notothenid fish Trematomus Nicolai. *The American Society of Ichthyologists and Herpetologists*, *2*, 320–327. https://doi.org/10.1643/CG-08-087

Kumar, S., Stecher, G., Suleski, M., Sanderford, M., Sharma, S., & Tamura, K. (2024). Molecular evolutionary genetics analysis version 12 for adaptive and green computing. *Molecular Biology and Evolution*, *41*, 1–9. https://doi.org/10.1093/molbev/msae263

Laptikhovsky, V. V. (2005). A trophic ecology of two grenadier species (Macrouridae, Pisces) in deep waters of the Southwest Atlantic. *Deep Sea Research*, *50*, 1502–1504. https://doi.org/10.1016/j.dsr.2005.03.003

Librado, P., & Rozas, J. (2009). DnaSP V5: A software for comprehensive analysis of DNA polymorphism data. *Bioinformatics*, *25*, 1451–1452. https://doi.org/10.1093/bioinformatics/btp187

McMillan, P., Iwamoto, T., Stewart, A., & Smith, P. J. (2012). A new species of grenadier, genus *Macrourus* (Teleostei, Gadiformes, Macrouridae) from the southern hemisphere and a revision of the genus. *Zootaxa*, *3165*, 1–24. https://doi.org/10.11646/zootaxa.3165.1.1

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., Hara, R. B. O., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2025). Vegan: Community ecology package. R package version 2.6.8. https://CRAN.R-project.org/package=vegan.

Pinkerton, M. H., McMillan, P., Forman, J., Marriott, P., Horn, P., Bury, S., & Brown, J. (2013). Distribution, morphology and ecology of *Macrourus whitsoni* and *M. caml* (Gadiformes, Macrouridae) in the Ross Sea region. *CCAMLR Science*, *20*, 37–61.

Queirós, J. P., Xavier, J. C., Abreu, J., Collins, M. A., Belchier, M., & Hollyman, P. R. (2024). What inhabits the South Sandwich Islands deep-sea? Biodiversity and biogeography of bathyal communities using predators as biological samplers. *Deep Sea Research Part I: Oceanographic Research Papers*, *205*, 104260. https://doi.org/10.1016/j.dsr.2024.104260

R Core Team. (2025). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org.

Roberts, J., Xavier, J. C., & Agnew, D. J. (2011). The diet of toothfish species *Dissostichus eleginoides* and *Dissostichus mawsoni* with overlapping distributions. *Journal of Fish Biology*, *79*, 138–154. https://doi.org/10.1111/j.1095-8649.2011.03005.x

Romero Martínez, M. L., Reid, W. D. K., Collins, M. A., Treviño Cuellar, K. L., Goodall-Copestake, W. P., Clark, J. M., Viney, B., Gregory, S., Owen, K., & Hollyman, P. R. (2026). What's inside the net? Insights into fish bycatch diversity in the Antarctic krill fishery. *Polar Biology*, *49*, 24. https://doi.org/10.1007/s00300-026-03463-4

Sanders, C. J., O'Hara, T. D., Guzzi, A., Goodall-Copestake, W. P., Convey, P., Narayanaswamy, B. E., Martín-Ledo, R., & Stöhr, S. (2025). And then there were many: Insights from the tangled taxonomy of the Antarctic brittle start *Ophioplinthus gelida* (Echinodermata: Ophiuroidea). *Frontiers in Marine Science*, *12*, 1615695. https://doi.org/10.3389/fmars.2025.1615695

Segovia, N. I., Gonzáles-Waver, C. A., Naretto, J., Rosenfield, S., Brickle, P., Hüne, M., Bernal, V., Haye, P. A., & Poulin, E. (2022). The right tool for the right question: Contrasting biogeographic patterns in the notothenioid fish *Harpagifer* spp. along the Magellan Province. *Proceedings of*

the Royal Society B: Biological Sciences, *289*, 20212738. https://doi.org/10.1098/rspb.2021.2738

Singh, M., Sharman, M., Singh, A. P., Mahajan, S. K., & Mishra, P. (2023). Modern techniques for identification of fishes. In P. R. Yadav, R. A. Balikai, & D. Sagar (Eds.), *Animal diversity: Taxonomical and physiological aspects* (pp. 131–141). M/S Academic Publishers & Distributors, Lucknow.

Smith, P. J., Steinke, D., McMillan, P. J., Stewart, A. L., McVeagh, S. M., Diaz de Astarloa, J. M., Welsford, D., & Ward, R. D. (2012). DNA barcoding highlights a cryptic species of grenadier *Macrourus* in the Southern Ocean. *Journal of Fish Biology*, *78*, 355–365. https://doi.org/10.1111/j.1095-8649.2010.02846.x

Smith, P. J., Steinke, D., McVeagh, S. M., & Stewart, A. L. (2008). Molecular analysis of Southern Ocean skates (*Bathyraja*) reveals a new species of Antarctic skate. *Journal of Fish Biology*, *73*, 1170–1182. https://doi.org/10.1111/j.1095-8649.2008.01957.x

Stevens, D. W., Dunn, M. R., Pinkerton, M. H., & Forman, J. S. (2014). Diet of Antarctic toothfish (*Dissostichus mawsoni*) from the continental slope and oceanic features of the Ross Sea region, Antarctica. *Antarctic Science*, *26*, 502–512. https://doi.org/10.1017/S095410201300093X

Suchard, M. A., Lemy, P., Baele, G., Ayres, D. L., Drummond, A. J., & Rambaut, A. (2018). Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10. *Virus Evolution*, *4*, vey016. https://doi.org/10.1093/ve/vey016

Tamura, K. (1992). Estimation of the number of nucleotide substitutions when there are strong transition-transversion and G + C- content biases. *Molecular Biology and Evolution*, *9*, 678–687. https://doi.org/10.1093/oxfordjournals.molbev.a040752

SUPPORTING INFORMATION

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

How to cite this article: Romero Martínez, M. L., Abreu, J., Queirós, J. P., Xavier, J. C., Hollyman, P. R., Fitzcharles, E., & Collins, M. A. (2026). DNA barcoding reveals the presence of Whitson's grenadier, *Macrourus whitsoni*, in sub-Antarctic waters of South Georgia, Southern Ocean. *Journal of Fish Biology*, 1–8. https://doi.org/10.1111/jfb.70577