

Distribution and ecology of the four *Macrourus* species by-caught in the longline fishery at South Georgia, Southern Ocean

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Abstract

Although *Macrourus* species are the main by-catch across Southern Ocean longline fisheries, including around South Georgia, the lack of species-specific data has hindered effective management and ecological understanding. Aggregation of macrourids at genus level masks critical interspecific differences in life-history strategies and vulnerabilities to fishing. Here, we provide the first comprehensive biological assessment of the four macrourid species caught in South Georgia waters: *Macrourus caml*, *Macrourus carinatus*, *Macrourus holotrachys* and *Macrourus whitsoni*. Using fishery and observer data collected in 2018–2022, we reveal pronounced female-biased sex ratios in three species (*M. holotrachys*, *M. carinatus* and *M. caml*), strong depth-based segregation by body length, distinct distributions and habitat preferences related to environmental features (bathymetric depth and slope, primary productivity and temperature). By-catch rates were highest in the southern region of South Georgia and varied across species: *M. holotrachys* was the most frequently caught and had a wide spatial and bathymetric distribution (~1000–1750 m); *M. caml* was the second most caught and appeared the most flexible in terms of habitat use; *M. carinatus* was mainly caught in the west, including at Shag Rocks; and *M. whitsoni* was caught less frequently and in deeper water (> 1500 m), mostly in the northeast and east, and had the most restricted distribution. These interspecific differences underscore the need for species-level assessments of fisheries risk and improved data collection to fill knowledge gaps. Overall, this study provides a critical foundation for understanding the ecology of *Macrourus* species in sub-Antarctic ecosystems and highlights that additional data are required for by-caught species to aid species-level management in toothfish longline fisheries in the CCAMLR area.

KEYWORDS

Antarctica, by-catch, deep-sea fisheries, grenadiers, management, species distribution model

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1 | INTRODUCTION

Global fisheries have undergone substantial changes over time, including an expansion into deeper waters during past decades (Haedrich et al., 2001; Morato et al., 2006). These changes, driven by factors that include poor management, lack of scientific knowledge and over-exploitation, have led fisheries to shift target species as stocks become depleted or unprofitable (Haedrich et al., 2001; Norse et al., 2012; Victorero et al., 2018). This includes fisheries in the Southern Ocean, although to a lesser extent than in other regions (Agnew, 2004; Everson, 1977). In the early years (1960s), when bottom trawling predominated, fishing mainly occurred in shelf waters, targeting species such as *Notothenia rossii*, *Patagonotothen guntheri* and *Champscephalus gunnari*, many of which are still recovering from that period of overexploitation (Hollyman et al., 2021; Trathan, 2023). By-catch during this phase mainly consisted of *Gobionotothen gibberifrons*, *Chaenocephalus aceratus* and other shallow demersal fish species (Agnew, 2004; Kock, 1992). However, the transition to longline fishing targeting toothfish (*Dissostichus* spp.) in the late 1980s led to a shift to deeper waters (500–2000 m). Although longlining is more selective than bottom trawling, these fisheries also catch non-target species such as skates and macrourids. Macrourids (grenadiers) are among the most abundant fish on deep continental slopes across the world (Cohen et al., 1990; Fricke et al., 2022; Iwamoto, 2008). They are occasionally targeted (e.g., *Macrourus berglax* in the North Atlantic and Barents Sea) and frequently by-caught in deep-sea fisheries, such as *Coryphaenoides acrolepis* in the Pacific Ocean and *Macrourus carinatus* in the southwest Atlantic Ocean (Bergstad et al., 2021; Porteiro et al., 2017).

In Southern Ocean longline fisheries, four species of the genus *Macrourus* (*Macrourus holotrachys*, *Macrourus carinatus*, *Macrourus caml* and *Macrourus whitsoni*) are recorded as by-catch. *M. caml* and *M. whitsoni* were considered a single species until mitochondrial DNA analyses revealed two distinct clades of *M. whitsoni*, leading to their reclassification in 2012 (McMillan et al., 2012; Smith et al., 2011). Currently, these four species constitute the main by-catch of all the longline fisheries for Patagonian and Antarctic toothfish (*Dissostichus eleginoides* and *Dissostichus mawsoni*, respectively) in the Southern Ocean, including at South Georgia, Kerguelen Islands, Crozet Islands, Heard Island and McDonald Islands (HIMI), Prince Edward Islands and the Ross Sea Region (CCAMLR, 2022b, 2022c, 2022d, 2022e, 2022f, 2022a; Gon et al., 2021). Macrourids were first reported in 1995 at South Georgia and later in other fisheries, with a cumulative catch of *Macrourus* spp. in the Southern Ocean of 27,991 tonnes, until 2022 (Table 1).

Fisheries in the Southern Ocean are managed under the Convention for the Conservation of Antarctic Marine Living Resources. This advocates an ecosystem-based management approach, which includes the setting of catch limits for target and non-target species within the Convention area (Constable, 2011; Constable et al., 2000; Hanchet et al., 2015; Trathan, 2023). Article II of the Convention aims not only to minimise the risk of depletion and to ensure sustainability of the target species but also to minimise effects on non-target species

(e.g., marine mammals, seabirds, fish) and the broader ecosystem. Despite this ambition, lack of knowledge has hindered the development of informed conservation measures, with several studies noting that the precautionary catch limits for macrourids (as taxa) are based on insufficient biological data (Grüss et al., 2023; Hanchet et al., 2008; Morley et al., 2004).

Macrourids, besides being the main by-catch, are also a major component of benthopelagic ecosystems across the Southern Ocean, both as prey (e.g., toothfish) and as predators of crustaceans, squid and fish (Morley et al., 2004; Pilling et al., 2001; Pinkerton et al., 2012; Queirós et al., 2025; Stevens et al., 2014). Macrourids inhabit a broad bathymetric range but are most common from 200 to over 2000 m deep, occupying upper continental shelf-slopes to upper hadal depths (Jamieson et al., 2021; Pinkerton et al., 2012; Smith et al., 2011). Able to grow to >70 cm total length (TL) and >4 kg, macrourids exhibit life-history characteristics consistent with other deep-sea fishes, including long life span (> 30 years), slow growth rates, delayed maturation and low natural mortality, making them particularly vulnerable to fishing (Lee et al., 2019; Moore et al., 2022; Morley et al., 2004).

The four macrourid species occurring in the Southern Ocean exhibit some regional segregation. *M. holotrachys* and *M. carinatus* are found predominantly north of 60°S, particularly around sub-Antarctic islands such as South Georgia, Heard and McDonald, Kerguelen, Crozet, Prince Edward and Macquarie islands (Gon et al., 2021; Gregory et al., 2017; Nowara et al., 2015; Pinkerton et al., 2013; van Wijk et al., 2003). *M. carinatus* is also abundant on the Patagonian Shelf (Laptikhovskiy, 2011; Lee et al., 2019). Both species are occasionally recorded close to Antarctica (Moore et al., 2022). By contrast, *M. caml* and *M. whitsoni* are more commonly found south of 60°S, particularly in the Ross Sea region, off Elephant and King George islands and Dronning Maud Land (Gon et al., 2021; Moore et al., 2022). *M. caml* also occurs in the sub-Antarctic, including at South Georgia (Gregory et al., 2017).

Over the past two decades and following the description of *M. caml* in 2012 (McMillan et al., 2012; Smith et al., 2011), the distributions of macrourids in the Southern Ocean have become better known (Fitzcharles, 2014; Gon et al., 2021). At South Georgia, previous studies of macrourids focused primarily on *M. holotrachys*, which is the most abundant species (Morley et al., 2004; Morley & Belchier, 2002). *M. whitsoni* was not considered to occur at South Georgia (Fitzcharles, 2014; Gon et al., 2021), likely due to limited sampling or misidentification, but its presence was recently confirmed by DNA barcoding (Romero Martínez et al., 2025), potentially representing the northernmost population. These few studies reflect the general lack of information on biology and ecology of the genus in this area (Grüss et al., 2023; Hollyman et al., 2022; Trathan, 2023). Currently, catch records are aggregated at the genus level, largely due to uncertainties in identification (Figure 1) (Gon et al., 2021; McMillan et al., 2012). This complicates efforts to evaluate species-specific fishing impacts, as it masks potential differences in life-history traits, abundance, habitat preferences and, therefore, vulnerability to fishing (Hollyman et al., 2022; Moore et al., 2022; Pinkerton et al., 2013). Our

TABLE 1 Summary of the distribution, by-catch limits and conservation measures (CM) applied to *Macrourus* species in Southern Ocean toothfish fisheries in 2022.

Location	CCAMLR area	Target species	Macrourus species	Total by-catch	Average catch (2018–2022)	By-catch limits	CM	References
South Georgia	48.3	TOP	4	1934 (since 1995)	94.6	5% <i>Dissostichus eleginoides</i> quota	CM41-02 (move on rule ^a)	CCAMLR, 2022a; this study
South Sandwich Islands	48.4	TOP & TOA	2 ^e	142 (since 2005)	6	16% <i>Dissostichus</i> spp. quota	CM 41–03 (move on rule ^b)	Fitzcharles 2014; CCAMLR, 2022g; Hollyman et al., 2022
Bouvet Island; Maud Rise and Astrid ridge	48.6	TOA	4 ^c	155 (since 2004)	10.6	16% <i>Dissostichus</i> spp. quota	CM 33–03 (move on rule ^a + cease fishery ^d)	Jones et al., 2008; Gon et al., 2021; Padilla et al., 2015; CCAMLR, 2022h
Mac. Robertson Land & Princess Elizabeth Land, shelves	58.4.2	TOA	4 ^e	88 (since 2003)	5.2	16% <i>Dissostichus mawsoni</i> quota	CM 33–03 (move on rule ^a)	CCAMLR, 2022i; Péron et al., 2018
Kerguelen Islands	58.5.1	TOP	4	15,387 (since 1998)	608.4	None established	French EEZ	CCAMLR, 2022b
Heard & McDonald Islands	58.5.2	TOP	4	3225 (since 1997)	<i>Macrourus caml</i> + <i>Macrourus whitsoni</i> = 74 <i>Macrourus holotrachys</i> + <i>Macrourus carinatus</i> = 165	<i>M. caml</i> + <i>M. whitsoni</i> = 409 <i>M. holotrachys</i> + <i>M. carinatus</i> = 360	CM 33-02 ^f (move on rule)	CCAMLR, 2022d; Dell et al., 2015 (WG-FSA-15/63)
Crozet Islands	58.6	TOP	4	2526 (since 1997)	67.2	None established	French EEZ	CCAMLR, 2022c
Prince Edward Islands	58.7	TOP	4	295 (since 1996)	12.2	?	South African EEZ	CCAMLR, 2022e; Gon et al., 2021
Ross Sea Region	88.1	TOA	4	3520 (since 1997)	139.2	16% <i>D. mawsoni</i> quota ^g	CM 41-09 ^g CM 33–03	CCAMLR, 2022f; Pinkerton et al., 2015; Moore et al., 2022
Amundsen Sea	88.2	TOA	4	682 (since 2003)	29.6	16% <i>D. mawsoni</i> quota ^g	CM 41–01 CM 33–03 (move on rule ^a + cease fishery ^d)	CCAMLR, 2022j
Bellingshausen Sea	88.3	TOA	2 ^e	37 (since 2016)	6.75	16% <i>D. mawsoni</i> quota ^g	CM 41–01 CM 33–03 (move on rule ^a + cease fishery ^d)	CCAMLR, 2022l

Note: All CCAMLR reports used date from 2022, and the conservation measures (CMs) apply to *Macrourus* spp. Fisheries in subareas 48.1 (Antarctic Peninsula), 48.2 (Antarctic Peninsula), 58.4.1 (D'Urville Sea), 58.4.3a (Elain Bank), 58.4.3b (Banzare Bank), 58.4.4a (Ob Bank) and 58.4.4b (Lena Bank) were excluded, as they were either inactive or closed by 2022. Catch measured in tonnes. EEZ: Exclusive Economic Zone.
^aIf the by-catch of any *Macrourus* species is equal to or greater than 1 tonne in any haul, trigger the move on rule: 'the fishing vessel must move at least 5 nautical miles away for a period of at least five days'.
^bIf the catch of *Macrourus* spp. reaches 150 kg and exceeds 16% of the catch of *Dissostichus* spp. in any haul, trigger the move on rule.
^cReferences only mention three species (*M. holotrachys*; *M. carinatus* and *M. whitsoni*) yet are prior to the description of *M. caml*. Due to location and near areas, some of the *Macrourus* identified might be *M. caml*.
^dIf during any two different 10-day periods in a single SSRU (where a catch limit is in place), a single vessel catches more than 1500 kg of *Macrourus* spp., and that amount is over 16% of the total *Dissostichus* spp. caught in that 10-day period, then the vessel must stop fishing in that SSRU for the rest of the fishing season.
^eAt subarea 48.4, *M. whitsoni* and *M. caml* are present, whereas in subareas 58.4.2 and 88.3, at least two species have been recorded so far, though it is uncertain whether more species are present or whether they were properly identified due to limited data.
^fIf the by-catch in any one haul is equal to or greater than 3 tonnes for all *Macrourus* spp. combined, the fishing vessel shall not use that method of fishing at any point within 5 n miles of that location.
^gBy-catch limits are dependent on small-scale research units.

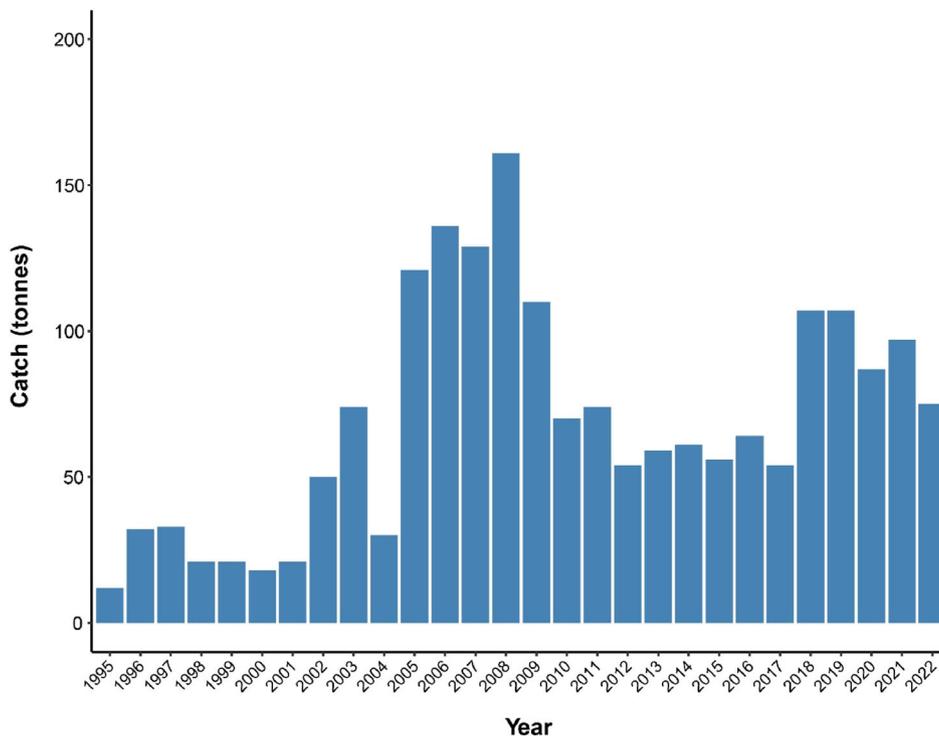


FIGURE 1 Reported catch of *Macrourus* spp. in the South Georgia (CCAMLR subarea 48.3) longline fishery since 1995.

study represents the first effort to determine the distributions, habitats and life-history characteristics of the four dominant macrourid species at South Georgia using species-level data collected between 2018 and 2022 from the longline fishery. Specifically, for each species we aimed to (1) quantify the relative contribution to by-catch, (2) evaluate species-specific relationships with environmental features at fished locations around South Georgia and (3) examine key biological parameters such as length, length-weight relationships, sex ratios and depth distribution. Our results provide the basis for improved species identification and enable the development of more effective management strategies for *Macrourus* species.

2 | MATERIALS AND METHODS

2.1 | Study region and fishery

South Georgia (54° S, 38° W) is in the Atlantic sector of the Southern Ocean and within the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) subarea 48.3 (Figure 2). It forms part of the Scotia Ridge, a submarine arc linking South America to the Antarctic Peninsula, and lies within the eastward-flowing Antarctic Circumpolar Current (ACC), south of the Antarctic Polar Front and north of the Southern boundary of the Antarctic Circumpolar Current (Atkinson et al., 2001; Orsi et al., 1995). The South Georgia shelf is characterised by steep bathymetric features, including deep gullies and abrupt shelf breaks (Young et al., 2014). Shag Rocks, a cluster of six islets located 240 km west of the main island group, are separated from the South Georgia continental shelf by a deep gully (1600–2000 m depth) and differ considerably in environmental conditions

(Cavanagh et al., 2024; Hollyman et al., 2021). These geographic and oceanographic conditions drive nutrient upwelling, resulting in productivity levels that far exceed those typical of the Southern Ocean, both around the island and downstream (Atkinson et al., 2001; Murphy et al., 2007). Consequently, the region is an important ecological hotspot and supports trawl fisheries for Antarctic krill (*Euphausia superba*) and mackerel icefish (*C. gunnari*), as well as a longline fishery for Patagonian toothfish.

The longline fishery at South Georgia has operated since 1988, with considerable changes in management, fleet and catch limits (Abreu et al., 2024; Bamford et al., 2024). The fishery currently operates from May to August (with occasional extensions in late April or early September) and now involves two to five vessels each season. Among the eight vessels active between 2018 and 2022, one operated with Spanish longline gear in 2018–2020, whereas all others exclusively used autoline gear (Collins et al., 2010). Since 2012, the longline fishery has been restricted to depths between 700 and 2250 m, but some shallow fishing research lines have been set from 500 to 700 m.

2.2 | Macrourid data

Data on macrourids caught in the South Georgia commercial fishery were obtained from two sources: CCAMLR vessel catch data (C2) and CCAMLR observer data (CCAMLR Data Requests # 609, 610 and 742). CCAMLR C2 is line-by-line data, which include the number of hooks set, date, latitude, longitude and depth. Our study focused on data from 2018 to 2022, which is the period when observers were provided with enhanced identification guides and asked to make a particular effort to identify macrourids to species level. Depth was

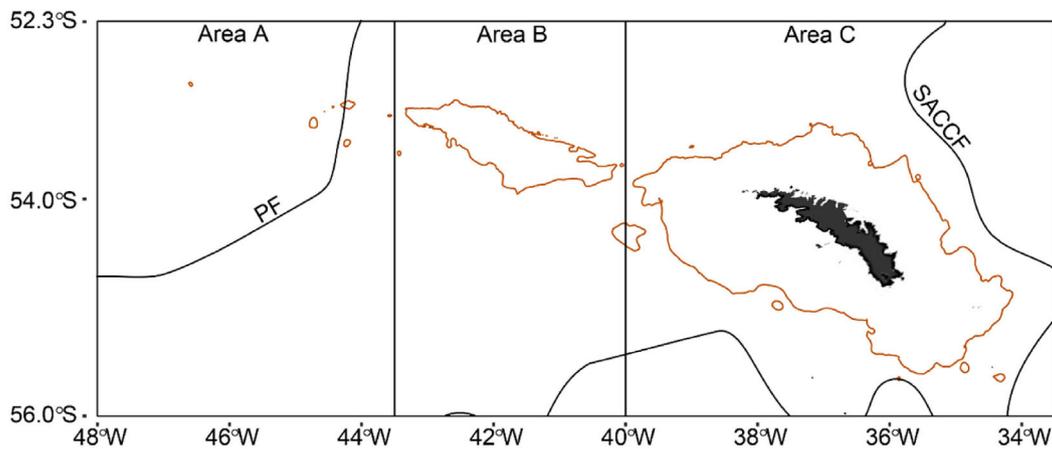


FIGURE 2 Map of South Georgia and Shag Rocks region (CCAMLR subarea 48.3). Each box represents the respective management areas (A–C). The orange line denotes the 1000 m bathymetric contour. The black lines labelled PF denotes the mean position of the Antarctic Polar Front, and labelled SACCF denotes the mean position of the Southern Antarctic Circumpolar Current Front (Orsi et al., 1995).

standardised as the midpoint between initial and final depths for each longline set and binned into five categories (<700, 700–1000, 1000–1200, 1200–1400 and > 1400 m). Under the CCAMLR Scheme of International Scientific Observation (CCAMLR, 2020), observers collect standardised biological data from each haul on target species, Patagonian toothfish and by-catch species, including macrourids. Following the Scheme, observers must collect data on up to five macrourid individuals on each line hauled. Macrourid data collection focused on species identification, total length (or pre-anal length, in cm) and weight (in kg), with some records of sex and maturity stage. This dataset included 23,120 individuals measured over the study period. However, data were incomplete (missing length, maturity, sex or weight) for 2237 fish, or were from outside the core fishing season of May to August for 1241 fish; these were therefore excluded from our analyses. In addition, fish identified only as *Macrourus* spp. were excluded from analyses other than those related to total catch.

2.3 | Statistical analysis of length distribution

Differences in length among species were examined using a one-way analysis of variance (ANOVA) followed by Tukey's multiple comparison test, whereas differences between sexes were evaluated using a two-sample *t*-test. Before ANOVA and post hoc tests we checked for normality and homogeneity of variance of length distribution data. All statistical (with $\alpha = 0.05$) and modelling analyses were carried out using R version 4.3.1 (R Core Team, 2023).

2.4 | Species habitat models

2.4.1 | Environmental data

Models were built to evaluate species-environment relationships using environmental covariates that reflected conditions during the

same 5-year period as available macrourid data, including sea-water temperature (hereafter: temperature) and salinity at various depth intervals, sea surface primary productivity, sea surface height, depth, slope (steepness) and slope aspect (direction) (Table S1). Given that macrourids are deep-sea species, these covariates were chosen for their relevance to this habitat or for habitat selection of marine ectotherms in general (Duhamel et al., 2014; Freer et al., 2019; Grüss et al., 2023; Moore et al., 2022; Morley et al., 2004). All covariates were extracted from cells within the fishing area (CCAMLR 48.3 management areas B and C; 33.30°W to 43.3°W and 52.3°S to 56°S) at a resolution of 0.083° × 0.083° (Table S1). Bathymetry for each location was extracted from the General Bathymetric Chart of the Oceans (GEBCO) (GEBCO Compilation Group, 2024), and both slope and slope aspect were calculated for each grid cell based on the surrounding topography. Values for temperature, salinity, primary productivity and sea surface height were extracted from the Copernicus Marine Service (doi.org/10.48670/moi-00021; doi.org/10.48670/moi-00015; see Table S1 for details). Temperature and salinity were extracted at depths corresponding to those in which macrourids are caught in the fishery (550–1800 m; see Table S2). All dynamic environmental covariates were averaged over May to August, and then over the 5-year period (2018–2022). Means of temperature and salinity were calculated for each of the seven depth layers (Table S2), and vertically integrated products were also calculated. These steps were performed using *raster* (Hijmans et al., 2024), *sp* (Pebesma & Bivand, 2005) and *ncdf4* (Pierce, 2024) R packages.

2.4.2 | Macrourid occurrence data

Our initial approach was to build species habitat models using macrourid presence-absence data within binomial generalised additive models (GAMs), utilising high resolution (0.083° × 0.083°) environmental covariates. However, this method proved unsuccessful due to the by-catch sampling protocol, as the presences and absences of

each species had high spatial overlap, preventing the differentiation of the environmental factors influencing spatial distribution. To overcome this, in place of presence–absence data, we used a metric of proportional occurrence calculated for each individual macrourid species. Additionally, if a species was recorded multiple times within a single line, only one occurrence was retained to represent that line (see schematic overview in Figure S1).

The study area (CCAMLR management areas B and C) was divided into grid cells of $0.25^\circ \times 0.25^\circ$ ($\sim 27.5 \times 16.3$ km). For each cell, the number of occurrences of the focal species was counted, and its proportion relative to the total occurrences was calculated (total occurrences: *M. holotrachys* - $n = 2860$; *M. caml* - $n = 696$; *M. carinatus* - $n = 329$; *M. whitsoni* - $n = 143$). The resolution of all environmental covariates was adjusted to match those of the macrourid data, that is, $0.25^\circ \times 0.25^\circ$, using bilinear interpolation within the *raster* R package. As such, this approach models the relationship between broadscale environmental conditions and the proportional occurrence of each species as by-catch around South Georgia.

2.4.3 | Model fitting and selection

Habitat models were developed for each macrourid species using GAMs within the *mgcv* R package (Wood, 2017). Prior to modelling, environmental covariates were tested for multicollinearity using variance inflation factor (VIF ≤ 5 was included; following Zuur et al., 2010). Sets of covariates were tested using temperature and salinity from each depth layer, and the set with lowest VIFs was selected (1245 m depth layer; Table S3). Correlation among selected covariates was examined using Pearson's correlation coefficients (correlation with $r > 0.7$ was excluded; Table S4), using the *usdm* R package (Naimi, 2017). As the response variable, occurrence proportion (range 0–1, represented by 0%–100%) was right-skewed and continuous, a Tweedie distribution with a log-link function was applied to each GAM. GAMs were fitted using a restricted maximum likelihood (REML) optimisation method to estimate splines, with penalised thin plate regression splines applied to all covariate smooth terms (Eilers & Marx, 1996). This allows for non-linear relationships between proportional occurrence and environmental covariates. To prevent overfitting, the number of basis functions (the variable k in the smoother function in *mgcv*) for each smooth was set to 4 and increased only when necessary based on the model diagnostics. Latitude and longitude were also included as terms (via a tensor smooth) to explicitly account for spatial autocorrelation in the model (Wood, 2017). Model assumptions were checked via examination of deviance residuals (distribution and pattern regarding model covariates) using the *gratia* R package (Simpson, 2024).

Model selection followed a backward stepwise selection procedure based on the Akaike Information Criterion (AIC), sequentially removing the least influential covariate until the most parsimonious model was determined (i.e., covariates removed until $\Delta\text{AIC} < 2$). When competing models had a $\Delta\text{AIC} < 2$, selection was based on the model with the fewer covariates, prioritising parsimony. This final GAM

allowed us to identify the environmental covariates most closely associated with higher by-catch proportions for each *Macrourus* species. Partial effect plots, showing the species–environment relationships fitted by the final model, were visualised using *gratia* R package. Comparisons of the model fitted versus empirically observed occurrence proportions of each species were also visualised using *ggplot2* package.

3 | RESULTS

3.1 | By-catch composition

In total, data were available for 19,642 individual macrourids during the fishing season (May–August) at South Georgia from 2018 to 2022, of which 18,585 were identified to species. *M. holotrachys* was by far the most by-caught species, accounting for over 80% of the by-catch by weight and over 70% of individuals in all years except 2022 (Figure 3). In 2022, 46% of all macrourids were only assigned to the genus. The second most frequently caught species was *M. caml* in 2020, 2021 and 2022, and *M. carinatus* in 2018 and 2019. *M. caml* and *M. carinatus* accounted for 4% to 11% and 1% to 13% by weight, and 4% to 16% and 1% to 15% by number of individuals, respectively, of the annual macrourid by-catch. *M. whitsoni*, which was the least abundant of the four macrourids at South Georgia, accounted for less than 2% of the weight in 2018–2021 and was not reported in our 2022 data (Figure 3).

3.2 | Species habitat models

The four final GAMs showed a good predictive performance. The model outputs and respective deviance explained and r^2 values (Tables 2 and S5–S8) confirmed that the various combinations of covariates were strong drivers of *Macrourus* distribution around South Georgia. Except for *M. whitsoni*, bathymetry had the greatest influence on habitat models (Table 2). Primary productivity was a significant covariate of distribution of all four species, slope for *M. holotrachys* and *M. whitsoni* and temperature for *M. caml* and *M. carinatus* (Table 2). The effects of slope aspect, sea surface height and salinity were weak or non-significant (Tables 2 and S5–S8). There were some discrepancies between the fitted and observed proportion of occurrence (Figure 4), for reasons discussed below.

The model predicted a widespread occurrence of *M. holotrachys* around South Georgia, with the highest proportions on the western shelf-break and the southern slope (Figure 4a). The model explained 47% of the deviance (Table 2). Bathymetry exhibited the strongest influence ($F = 11.437$, $p < 0.001$) and indicated higher occurrence in depths between 1250 and 1500 m (Figure S2). Primary productivity and slope were also significant covariates ($p \leq 0.01$), with a higher proportion of occurrence expected in areas of increased productivity and moderate seabed inclination (Figure S2).

FIGURE 3 Proportion of *Macrourus* (by weight) species (identified to species or genus level) by-caught in the South Georgia (CCAMLR subarea 48.3) longline fishery from 2018 and 2022.

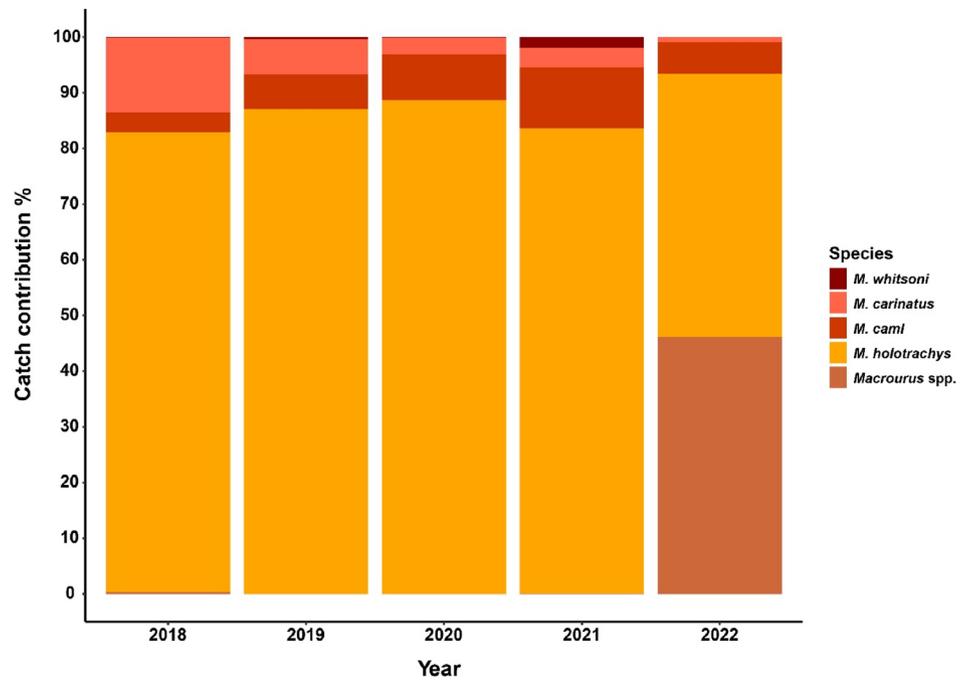


TABLE 2 Contribution of the environmental covariates to the final generalised additive model (GAM) for each macrourid species selected through a backward stepwise approach.

Species	Term	Estimate	St. error	EDF	Ref DF	F-value	p-Value	AIC	r ²	Dev. Expl.
<i>Macrourus holotrachys</i> (n = 122)	Intercept	-5.086	0.072				< 0.001			
	Bathymetry			2.716	2.936	11.437	< 0.001			
	Lon × Lat			6.123	7.048	5.190	< 0.001	-977.411	0.386	47.0%
	Primary productivity			2.236	2.610	6.009	0.001			
	Slope			2.570	2.862	6.327	0.002			
<i>Macrourus caml</i> (n = 79)	Intercept	-4.708	0.065				< 0.001			
	Bathymetry			1.311	1.552	9.469	< 0.001			
	Lon × Lat			3.001	3.001	13.053	< 0.001	-604.844	0.537	61.6%
	Primary productivity			2.130	2.536	9.546	< 0.001			
	Sea water temperature			2.426	2.778	8.591	< 0.001			
<i>Macrourus carinatus</i> (n = 71)	Intercept	-4.545	0.070				< 0.001			
	Bathymetry			1.567	1.903	5.929	0.004			
	Lon × Lat			8.760	10.729	2.833	0.006	-508.118	0.263	52.8%
	Primary productivity			2.477	2.746	3.007	0.027			
	Sea water temperature			1.000	1.000	4.481	0.039			
<i>Macrourus whitsoni</i> (n = 55)	Intercept	-4.176	0.068				< 0.001			
	Bathymetry			1.000	1.000	3.088	0.086			
	Lon × Lat			6.265	7.137	6.079	< 0.001	-366.726	0.308	61.9%
	Primary productivity			1.313	1.533	5.782	0.032			
	Slope			2.391	2.741	3.809	0.025			

Note: Covariate acronyms are as follows: longitude (Lon); latitude (Lat). The resulting coefficients of the model were used to generate the spatial projection (Figure 4).

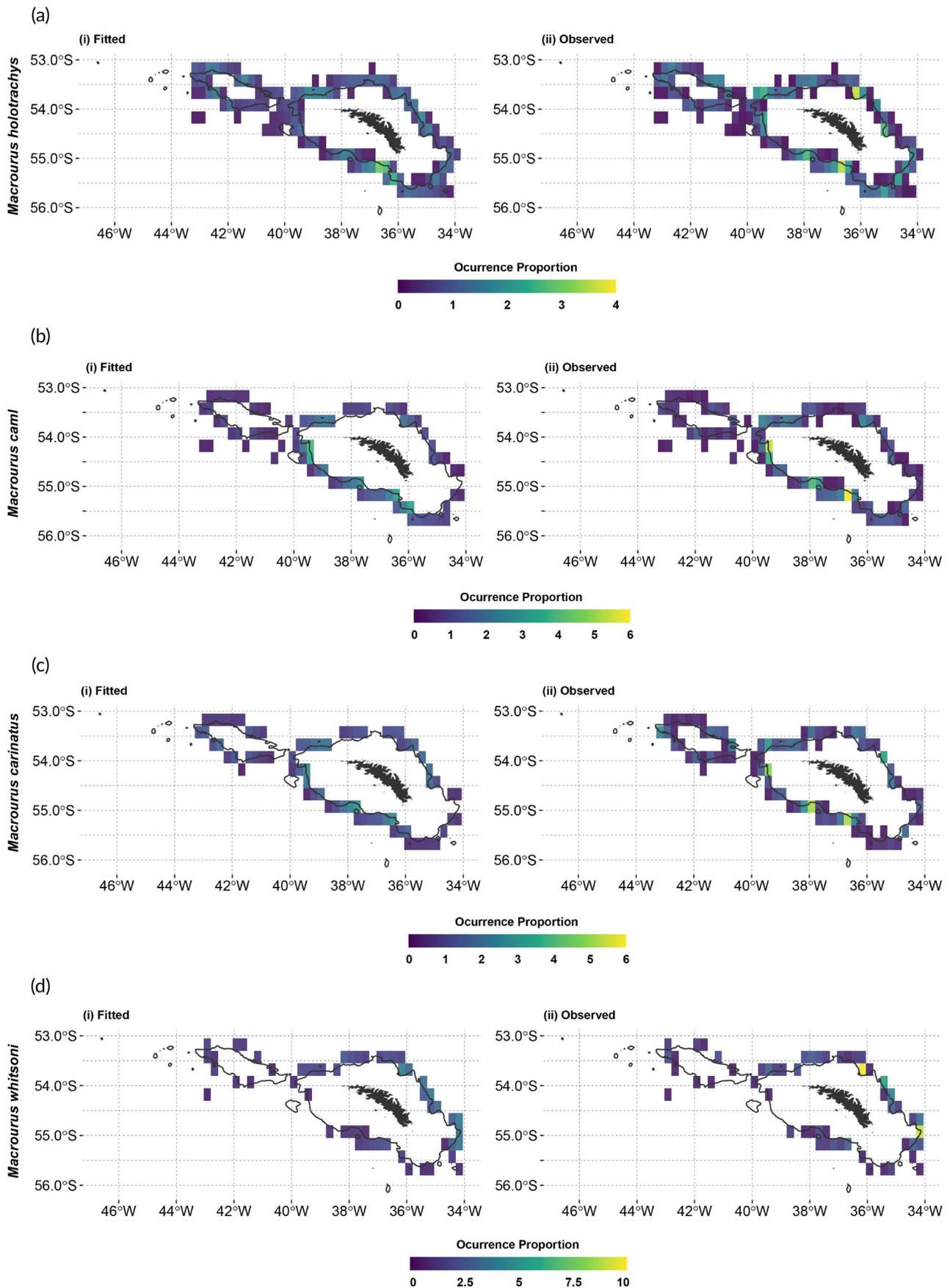


FIGURE 4 Legend on next page.

For *M. caml*, the fitted model predicted a higher proportion of occurrence along the southern and southeastern slopes of South Georgia and fewer occurrences in northern areas (Figure 4b). This was confirmed in the observed data (Figure 4b), showing the significant influence of the spatial term ($F = 13.053$, $p < 0.001$; Table 2). The model explained 61.6% of the deviance, with bathymetry as a key driver ($F = 9.469$, $p < 0.001$). Unlike *M. holotrachys*, *M. caml* was predicted to prefer shallower depths (< 1250 m) (Figure S3). Proportion of occurrence was also predicted to be higher in areas of higher productivity and lower temperatures (Figure S3).

For *M. carinatus*, the fitted model predicted a higher proportion of occurrences along the western and southwestern regions of South Georgia, including Shag Rocks (Figure 4c). Observed data generally corroborated this pattern but showed broader spatial dispersion (Figure 4c). The model explained 52.8% of the deviance; again, depth was significant ($F = 5.929$, $p = 0.004$), although less than for *M. holotrachys* or *M. caml*, and indicated that *M. carinatus* preferred shallower depths (Figure S4; Table 2). Proportion of occurrence showed a bell-shaped relationship with primary productivity, with a higher proportion of occurrence predicted to occur around ~ 110 mg C m². Similar to *M. caml*, *M. carinatus* was more likely to occur in colder waters (Figure S4).

For *M. whitsoni*, a high proportion of occurrences was mainly predicted along the northern and eastern edges of the study region and lower proportions towards the west (Figure 4d). Primary productivity ($F = 5.782$, $p = 0.032$) and slope ($F = 3.809$, $p = 0.025$) were significant covariates for *M. holotrachys*. Bathymetry was not statistically significant in the habitat model ($p = 0.086$), although the tendency was opposite to the other species in that the proportion of occurrence of *M. whitsoni* was higher at depths exceeding 1500 m (Figure S5).

3.3 | Sex ratios

Females generally predominated at most depths, and males constituted a smaller fraction of the by-catch across the four species (Figure 5). However, the proportion of males varied substantially among species and depth bins (Figure 5). In *M. holotrachys*, females dominated at all depths, with males consistently comprising less than 10% of the catch. *M. carinatus* displayed a similar pattern, albeit with a slightly higher proportion of males (10%–20%), particularly at shallower depths. In contrast, female *M. caml* were more frequent in shallower waters, and the proportion of males increased substantially with depth, reaching approximately 40%–50% in deeper waters (> 1400 m). This uneven sex ratio was confirmed by the χ^2 : $p < 0.001$ for these three species. *M. whitsoni* exhibited a more balanced sex ratio (χ^2 : $p = 0.749$), with males exceeding 50% at depths shallower

than 1000 m and approaching parity in deeper waters, a pattern not observed in the other species (Figure 5).

3.4 | Length patterns

Overall, the length distributions revealed a consistent size hierarchy among the four species; *M. holotrachys* was the largest (maximum length 90 cm TL; maximum weight 5.2 kg), followed by *M. caml* (maximum length 90 cm TL; maximum weight 4.2 kg), *M. carinatus* (maximum length 85 cm TL; maximum weight 4.5 kg) and *M. whitsoni* (maximum length 72 cm TL; maximum weight 2.7 kg) (Figure S6). There was significant sexual size dimorphism, particularly in *M. holotrachys*, *M. carinatus* and *M. caml* (Figure 6). Females of *M. holotrachys*, *M. caml* and *M. carinatus* were significantly bigger (by 22%, 13% and 12%, respectively) than males (t -test, $p < 0.001$) (Figure 6). *M. whitsoni* was the smallest macrourid species, and there was no significant difference in the mean length of males and females (t -test, $p = 0.129$).

M. holotrachys and *M. caml* exhibited broader length distributions than *M. carinatus* and *M. whitsoni* (Figure 7). Total lengths of *M. holotrachys* and *M. carinatus* increased with depth for both sexes, particularly for females (Figure 7; Table S9), whereas males showed a narrower length range. In contrast, for *M. caml* and *M. whitsoni*, the trend in size with depth was less pronounced or absent (Figure 7). In all species except for *M. whitsoni*, females were significantly larger than males across all depth bins (two-sample t -test, $p < 0.001$; Table S9). This effect was especially evident in *M. holotrachys*, where length differences between sexes became more pronounced at greater depths. A similar, but less distinct, pattern was observed in *M. carinatus*, but not in *M. whitsoni*; in the latter species, lengths of both females and males were relatively consistent across depth bins (Figure 7, Table S9). Accordingly, macrourid females had wider depth distributions overall (Figure S7).

4 | DISCUSSION

Previous studies of the longline fisheries in the Southern Ocean, including around South Georgia, have largely focused on the ecology, biology and effects of fishing on the target species (Patagonian and Antarctic toothfish) (Abreu et al., 2024; Bamford et al., 2024; Collins et al., 2010; Hanchet et al., 2015; Péron et al., 2016; Roberts et al., 2011; Seong et al., 2023; Yates et al., 2019). Far less attention has been directed to by-catch, particularly at the species level (Gon et al., 2021; Moore et al., 2022; Pinkerton et al., 2015). Here, we present the first dedicated study into the biology, distribution and habitat

FIGURE 4 Generalised additive model (GAM) predicted proportion of occurrence (i) versus the observed proportion of occurrence from fishery data (ii) for each macrourid species at South Georgia: (a) *Macrourus holotrachys*, (b) *Macrourus caml*, (c) *Macrourus carinatus* and (d) *Macrourus whitsoni*, in the 5-year study period. Each species' map has its own occurrence scale (proportion, %), with all grid cells summing to 100%. Black line represents the 1000 m isobath.

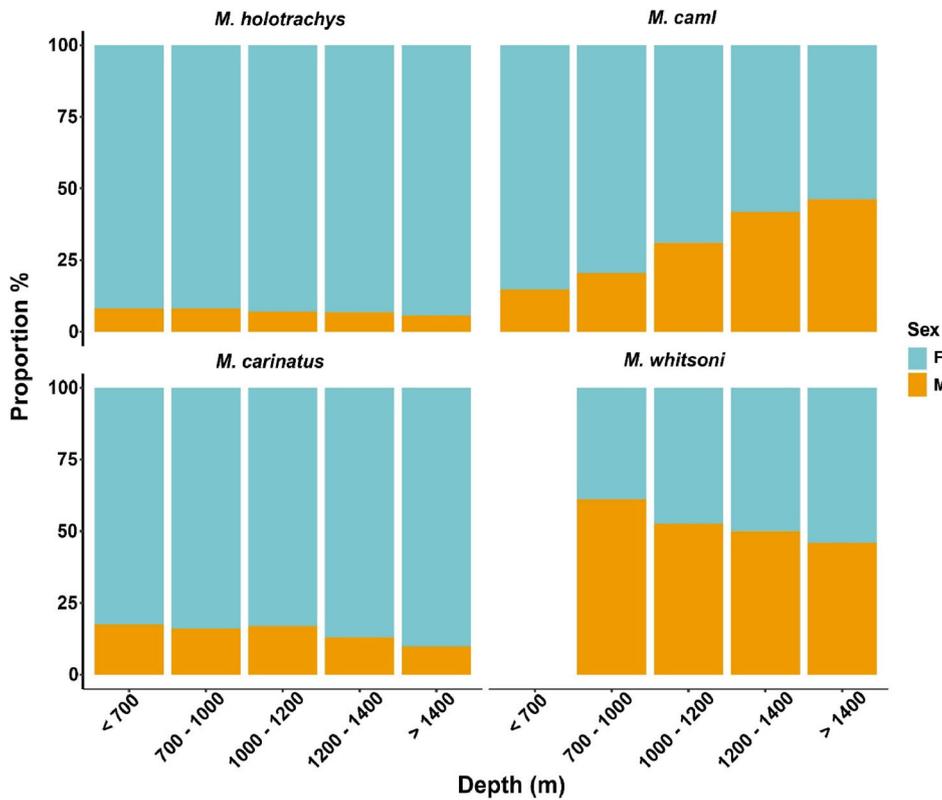


FIGURE 5 Proportion (%) of females (F) and males (M) across depth (m) of the four *Macrourus* species by-caught at South Georgia (CCAMLR subarea 48.3) longline fishery from 2018 to 2022.

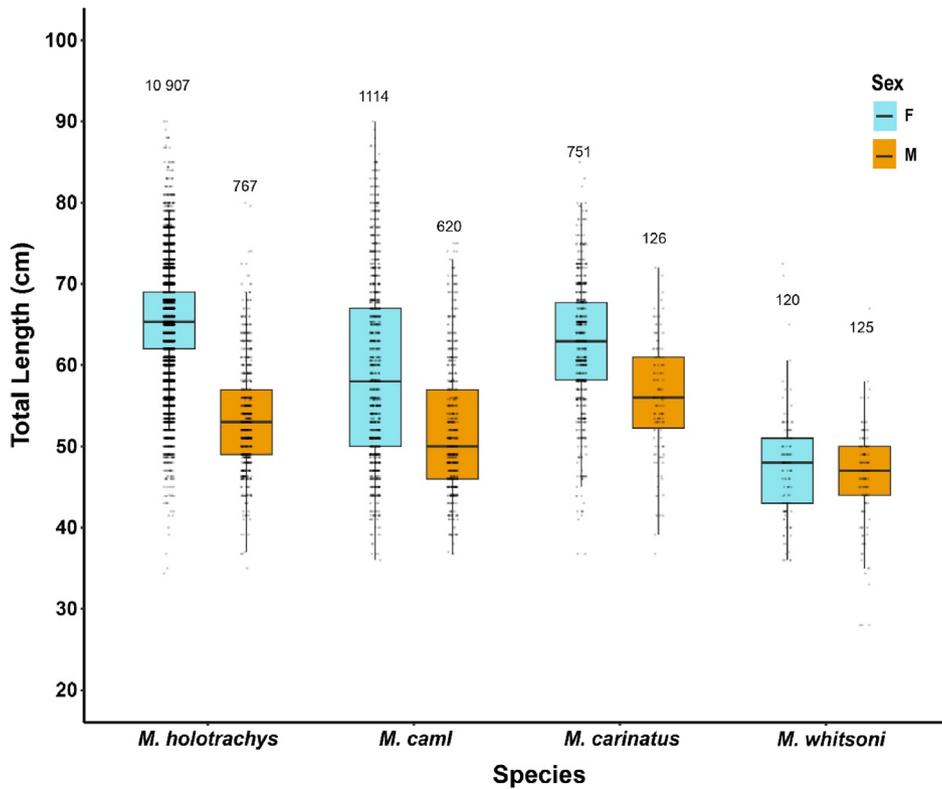


FIGURE 6 Length (cm) of females (F) and males (M) of the four macrourid species by-caught at South Georgia (CCAMLR subarea 48.3) longline fishery from 2018 to 2022. Values represent the number of individuals.

use of the various *Macrourus* species at South Georgia. Our results show that *M. holotrachys* is consistently, and by a wide margin, the most frequently by-caught species, and that there is a pronounced female-biased sex ratio as well as considerably larger body size in

females. Habitat models indicated clear, species-specific patterns in habitat use, though we acknowledge several data and sampling limitations (see below). Furthermore, our study confirms that all four Southern Ocean *Macrourus* species (i.e., *M. holotrachys*, *M. caml*,

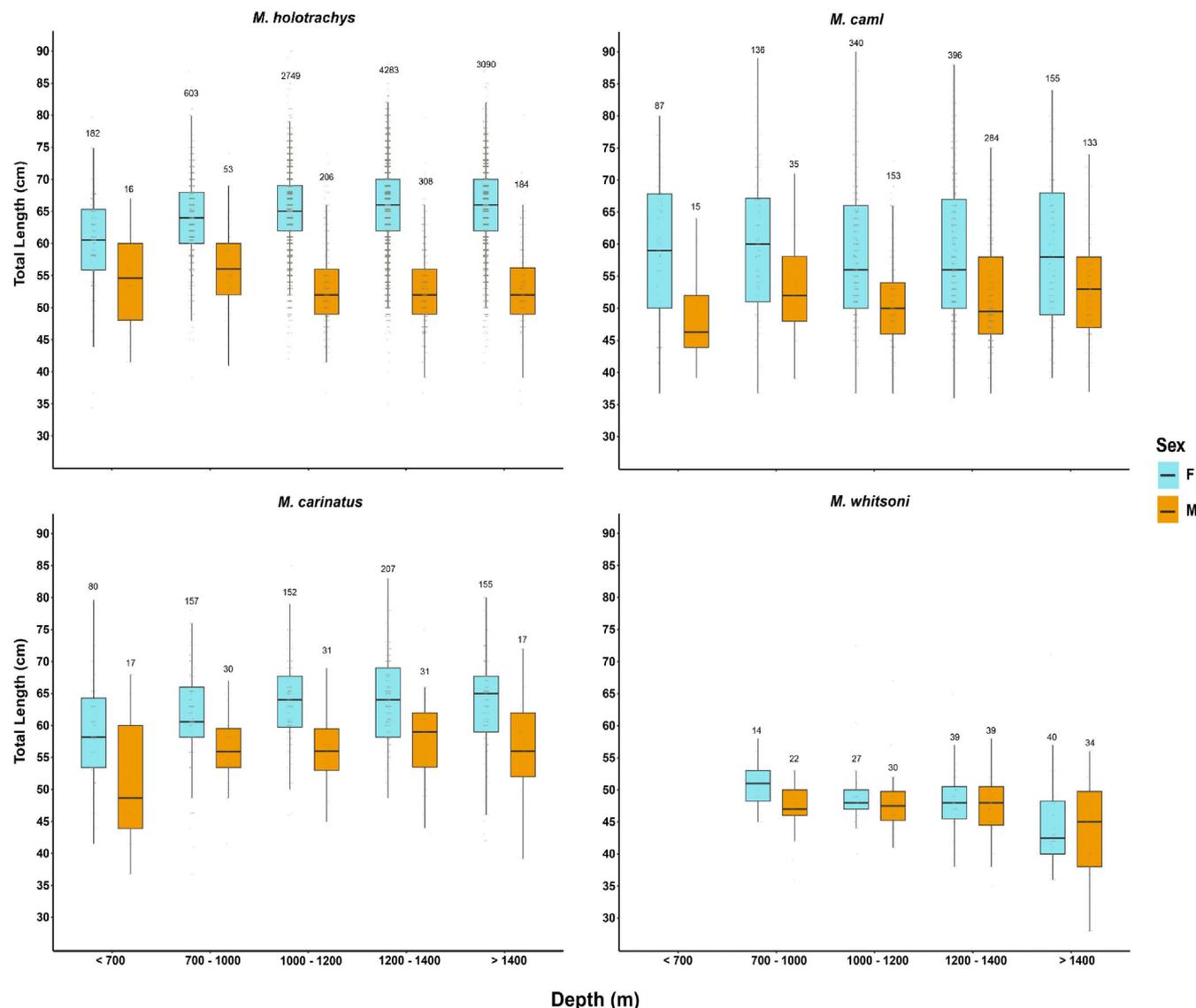


FIGURE 7 Boxplots of the total length (cm) of females (F) and males (M) of the four macrourids species by-caught at South Georgia (CCAMLR subarea 48.3) across depth (m). The number on top of each box corresponds to the respective sampled individuals.

M. carinatus and *M. whitsoni*) occur in South Georgia waters. Our results not only provide a better understanding of the deep-sea ecosystem in this remote region but also have important implications for macrourid conservation and management in the toothfish fisheries.

4.1 | Data and model limitations

Although sampling was spatially well distributed around South Georgia during the study period (Bamford et al., 2024), it is crucial to recognise that these *Macrourus* by-catch data originate from a fishery rather than dedicated scientific surveys such as those conducted for Antarctic krill or icefish (Fielding et al., 2014; Gregory et al., 2019). Consequently, there are some limitations.

A first is linked to how the data were collected, which is dependent on the implementation of CCAMLR protocols by individual

observers. For instance, due to the random sampling of macrourids, all five sampled individuals may be of a single species (usually *M. holotrachys*), and so other species present at that location may be missed. Moreover, because the observers mainly focus on toothfish (target species), their effort is concentrated during periods when toothfish are caught. Consequently, if macrourids are caught at different periods (e.g., if toothfish is caught earlier in the longline set and macrourids later, or vice versa), their probability of being sampled is lower. As a result, a standard presence-absence approach for abundance estimation is not feasible, as recorded absences may not be true absences.

A second limitation relates to the sampling method itself. The fishery operates at depths >700 m, and therefore, sampling is inherently biased towards larger specimens (discussed below).

A third limitation lies in incomplete sampling. The vessel-reported (C2) data include the total number of individuals caught and

extrapolate the total macrourid catch at the genus level from the weight of the five individuals sampled by the observer. Consequently, we were unable to determine species-specific catch per unit effort and associated spatial distribution. Given these limitations, we adopted an occurrence proportion approach, wherein we considered only one individual per species per line haul. This approach reduces bias towards heavily sampled or fished areas.

Nevertheless, the spatial predictions generated by the GAMs are still likely to be biased towards areas of high macrourid catches on the shelf-break. Although these predictions are robust within the sampled area, as evidenced by r^2 and substantial deviance explained by the models, substantially shallower or deeper habitats outside the fishing grounds, which may be vital to the life cycles of macrourids, were not represented. As such, the full extent of macrourid species distribution at South Georgia remains unknown. Future work could usefully expand sampling beyond the depths and areas targeted by longline fisheries to capture the broader environmental conditions influencing macrourid distributions. Despite these uncertainties, the occurrence data are still useful to indicate where each macrourid species is most likely to occur in the fishery.

4.2 | Macrourid catch

Macrourids are the main by-catch in all toothfish fisheries in the Southern Ocean, including at South Georgia, where they accounted for 67% (by weight) of all longline by-catch over the 5-year study period (2018–2022), which is less than reported for other regions, including the Ross Sea (77%) and Kerguelen Islands (88%) (CCAMLR, 2022f, 2022b; Grüss et al., 2023). However, skates in good condition are released alive and therefore total skate by-catch (in weight) reported is much less than the actual catch. The macrourid by-catch limit has remained relatively stable throughout the study period (2018–2022) as a fixed 5% of the toothfish catch limit (Abreu et al., 2024; CCAMLR, 2022a). The general practice of CCAMLR observers to report macrourid catches at the genus level (see Table 1) masks substantial interspecific differences in distribution, length, depth preferences and sex ratios, which directly influence vulnerability to fishing. Therefore, our study very clearly highlights the necessity for species-specific identification to properly implement an ecosystem-based approach towards management of the CCAMLR fisheries.

Among the four macrourid species found at South Georgia, *M. holotrachys* was the dominant by-caught species, consistently exceeding the collective catch contributions of *M. caml*, *M. carinatus* and *M. whitsoni* (Figure 3). *M. holotrachys* was also the largest and heaviest macrourid in the region (Figure 6, Morley et al., 2004, Fitzcharles, 2014), contributing more to the catch weight. This prevalence is likely driven by (i) ecological factors, such as the widespread distribution (see Section 4.3) and high abundance around South Georgia (hinted by previous studies at this location and other sub-Antarctic islands; Morley et al., 2004; Fitzcharles, 2014; Gon et al., 2021; CCAMLR, 2022a, 2022b, 2022c), and (ii) by the fishery

characteristics, which typically focus on depths between 1200 and 1300 m (Abreu et al., 2024; Bamford et al., 2024), where *M. holotrachys* is presumably more common (Figure 7, Laptikhovskiy, 2005, 2011), coupled with bait and hook size that attract larger macrourids (Yau et al., 2002). As a result, *M. holotrachys* may face disproportionate fishing mortality relative to the other macrourid species, an effect that would remain undetected under genus-level reporting.

Despite its stronger presence in higher latitudes, such as the Ross Sea region (Grüss et al., 2023; McMillan et al., 2012; Moore et al., 2022), *M. caml* was the second most frequent macrourid in catches. In many other sub-Antarctic fisheries, *M. holotrachys* and *M. carinatus* typically predominate, which may reflect their location north of the Antarctic Polar Front, whereas South Georgia lies to the south, potentially influencing the abundance of *M. caml* (CCAMLRb,c; Fitzcharles, 2014; Gon et al., 2021). As *M. caml* was only described as a new species in 2012 (McMillan et al., 2012; Smith et al., 2011), it was presumably misidentified as a different species (depending on the region) in previous years. In the Ross Sea, for example, it was misidentified as *M. whitsoni* (Moore et al., 2022; Pinkerton et al., 2012), whereas at South Georgia, it may have been recorded as *M. holotrachys*, *M. carinatus* or *M. whitsoni* (Fitzcharles, 2014; Gon et al., 2021; Laptikhovskiy et al., 2014). Such inaccuracies, both past and present, underscore how crucial proper species-level identification is for understanding true occurrence patterns.

M. carinatus was the third most frequent species by-caught, likely tied to its higher occurrence in shallower depths (Laptikhovskiy, 2005, 2011) and stronger presence around Shag Rocks and western South Georgia (see Section 4.3); these regions were subjected to lower fishing effort (hooks per km²) both during our 5-year period and historically (Bamford et al., 2024; Laptikhovskiy et al., 2014). In contrast to our study area, *M. carinatus* appears to be more abundant at other sub-Antarctic islands (CCAMLR, 2022b, 2022c; Gon et al., 2021) and on the Patagonian Shelf (Laptikhovskiy, 2011; Lee et al., 2019). One possible explanation is greater interspecific competition from *M. holotrachys* and *M. caml* at South Georgia (Laptikhovskiy, 2005; Laptikhovskiy et al., 2014; Moore et al., 2022). A second possibility is the location of South Georgia south of the Antarctic Polar Front, in contrast to most other sub-Antarctic islands which are to its north (van Wijk et al., 2010). Lastly, *M. whitsoni* contributed minimally to total macrourid by-catch. Consequently, its low contribution to the by-catch total is likely driven by both limited overlap with the fishery and underlying biogeographical constraints (Figure 4d, see Section 4.3).

Accurate identification by observers is crucial for reliable catch reporting, stock assessments and improved by-catch management (Beerkircher et al., 2009; Williams et al., 2018). This challenge of observer identification was particularly apparent in 2022, when the fishery opened in mid-June, later in the year than normal due to political constraints (Arpi & McGee, 2022). Although observers covered all the routine tasks in full, there was less opportunity to train observers to identify macrourids to species level. As a result, observers defaulted to '*Macrourus* spp.' rather than identification to species level, as in our other study years.

Excluding 2022, the lowest representation of *M. holotrachys* over the 5-year period was 82.5% of all macrourids caught, which would amount to ~350 t of the 473 t of macrourids reported from 2018 to 2022 (CCAMLR, 2022a), exceeding prior estimates (Morley et al., 2004; Morley & Belchier, 2002). The trend of increasing macro-urid catches is also observed in other fisheries managed by CCAMLR (Palomares & Pauly, 2011; Stevenson et al., 2014), likely driven by multiple factors, such as the shift from Spanish to autoline gear (which tends to have higher macro-urid by-catch rates; Laptikhovskiy et al., 2014), improved recording by observers and lower predation pressure given the reduced abundance of the main predator, Patagonian and Antarctic toothfish.

4.3 | Spatial distribution

Our results are the first comprehensive, species-level analysis of *Macrourus* distribution around South Georgia. Overall, spatial and environmental gradients shaped macro-urid occurrence, with higher proportions for all macro-urid species, except *M. whitsoni*, detected in the southern region of South Georgia, corroborating the conclusions for *Macrourus* spp. by Laptikhovskiy et al. (2014). *M. holotrachys* and *M. caml* were predicted to be widely distributed, whereas there was a higher proportion of occurrence of *M. carinatus* to the west and southwest of South Georgia, and *M. whitsoni* was restricted largely to the east and northeast. The widespread distribution pattern of *M. holotrachys* agrees with the only previous single-species study at South Georgia (Morley et al., 2004). It is noteworthy that the distribution patterns of the macro-urids contrast with the more northerly distribution of skates, which are the other main by-catch taxa at South Georgia (Laptikhovskiy et al., 2014).

Depth, primary productivity, slope and temperature at depth were the four main environmental drivers of macro-urid distribution, although the relative importance varied among species models. Previous studies in the Ross Sea region indicated that similar factors influenced habitat preference for *Macrourus* spp. (Grüss et al., 2023; Moore et al., 2023). *M. holotrachys* was predicted to be found in higher proportions between 1000 and 1750 m depth and was very uncommon in deeper water. That likely explains why it is caught more frequently than other species, given that the fishery mostly targets Patagonian toothfish at those depths (Morley et al., 2004; Laptikhovskiy, 2005; Abreu et al., 2024; Bamford et al., 2024, this study). *M. caml* and *M. carinatus* favoured slightly shallower depths (approximately 750–1250 m), consistent with records in other Antarctic regions (Lee et al., 2019; Moore et al., 2023; van Wijk et al., 2003). *M. whitsoni* had the highest relative representation of the four macro-urid species at depths >1500 m, which explains the positive relationship between depth and proportion of occurrence (Moore et al., 2023; Pinkerton et al., 2012, 2013).

The positive association with relatively high primary productivity values for all four species aligns with results from other sub-Antarctic regions, where macro-urids, as well as other taxa, tend to aggregate

near productive foraging grounds (Grüss et al., 2023). With a generalist diet, including both predation and scavenging, macro-urids are likely to favour such areas, attracted by zoo-planktivorous species (Morley et al., 2004; Pinkerton et al., 2012). Moderate-to-steep shelf breaks appear to represent favourable habitat for *M. holotrachys* and *M. whitsoni*, consistent with patterns observed elsewhere (CCAMLR, 2022d; Gon et al., 2021; Pinkerton et al., 2013). *M. carinatus* is predicted to tolerate a slightly higher temperature range than other species, in line with its more sub-Antarctic distribution (CCAMLR, 2022d; Gon et al., 2021; Lee et al., 2019; McMillan et al., 2012).

M. holotrachys had a near-ubiquitous presence around South Georgia (Figure 4a). Simultaneously, alongside its wider distribution, *M. caml* showed a strong association with waters off south-western South Georgia. Although *M. caml* has been mostly considered a higher-latitude species, inhabiting waters near Antarctica (Gon et al., 2021; Moore et al., 2023; Pinkerton et al., 2013), it may be the most habitat flexible of the macro-urid species, as it can thrive in both Antarctic and sub-Antarctic regions (Dell et al., 2015; Gon et al., 2021; Hollyman et al., 2022, this study). That potentially explains why it outnumbers *M. whitsoni* in areas outside the Ross Sea (Dell et al., 2015; Gregory et al., 2017, this study). *M. caml* and *M. whitsoni* exhibit overlapping distributions in the Ross Sea (Moore et al., 2022; Pinkerton et al., 2013), yet at South Georgia they appear to be largely segregated (Figure 4b,d), as they are found to be in the South Sandwich Islands (Hollyman et al., 2022; Queirós et al., 2024).

In contrast, *M. carinatus* was concentrated in western and south-western areas, particularly towards Shag Rocks (Fitzcharles, 2014). Our fitted model predicted lower occurrence of *M. carinatus* in the southern area in comparison to the observed data, possibly reflecting the fishery operations or other finer-scale environmental variation not fully captured by the main covariates. Finally, *M. whitsoni* has the narrowest distribution around South Georgia, preferentially occupying deeper waters in the east and northeast. Although previous reports suggested *M. whitsoni* is confined to Antarctic waters (Fitzcharles, 2014; Gon et al., 2021), we can now confirm that it occurs at South Georgia (Romero Martínez et al., 2025), albeit at low abundance in what are presumably suboptimal conditions. South Georgia may represent the northern limit of its range because environmental conditions are suboptimal for growth or – given its smaller size – it is outcompeted by other macro-urids, akin to distribution patterns at the north of the South Sandwich Islands (Fitzcharles, 2014; Hollyman et al., 2022; Queirós et al. 2024). A similar situation is assumed for mackerel icefish (*C. gunnari*), for which South Georgia and Shag Rocks are the northern limit (Morley et al., 2014).

Our species-level analysis reveals a mosaic of partially overlapping but distinct distributions at South Georgia driven by both environmental covariates and likely fishery dynamics. Although local anomalies and fishing effort patterns occasionally resulted in mismatches between predicted and observed occurrence, the underlying habitat relationships were robust.

4.4 | Sex ratios

There was a consistently significant female bias in sex ratios in three of the four macrourid species, most pronounced in *M. holotrachys* (14:1) and *M. carinatus* (6:1), in which >80% of individuals in nearly all depth bins were females. In contrast, female *M. caml* (2:1) were dominant in shallower waters, and males increasingly common in waters >1400 m, reaching near parity at the greatest depths. The sex ratio was broadly even in *M. whitsoni* across all depth strata. Female-biased sex ratios appear to be the norm for macrourids, including in previous studies at South Georgia (e.g., *M. holotrachys*; Morley & Belchier, 2002; Morley et al., 2004) and in other toothfish fisheries [e.g., *M. caml* and *M. whitsoni* at the Ross Sea (Hanchet et al., 2008; Moore et al., 2022; Pinkerton et al., 2012; Pinkerton et al., 2015), and *M. carinatus* at HIMI (van Wijk et al., 2003)]. Female-biased sex ratios have also been observed in *M. carinatus* on the Patagonian Shelf (Laptikhovskiy, 2005), *M. berglax* in the North Atlantic (Murua, 2003) and five other macrourid species in the Mediterranean Sea (D'Onghia et al., 2000; Massutí et al., 1995).

Multiple factors may lead to uneven sex ratios, including gear selectivity, sex-specific habitat use and differences in growth or mortality rates (Hanchet et al., 2008; Morley et al., 2004; Murua, 2003; van Wijk et al., 2003). Our results for *M. holotrachys* and *M. carinatus* probably reflect multiple factors: (i) females are generally larger than males (growth disparity); (ii) this size disparity is linked to deeper depths (i.e., larger fish inhabit deeper areas), where fishing effort is highest and (iii) larger individuals are more likely to swallow baited hooks (Yau et al., 2002). By contrast, *M. caml* and *M. whitsoni* showed more moderate size differences between sexes and limited depth segregation, and consequently, little or no female bias in the catch. Moreover, *M. whitsoni* caught at South Georgia is smaller than other macrourid species in the area and populations of this species elsewhere (Pinkerton et al., 2013; Moore et al., 2022, this study), which may reduce its likelihood of being caught on longlines. Many deep-sea fishes switch from predation at small sizes (and shallower depths) to scavenging at larger sizes (in deeper waters) and are thus more likely to take a bait (Collins et al., 2005). Other factors that could explain the sex-biased captures include migration timing, longevity or seasonal shifts in distribution (Laptikhovskiy, 2005, 2011; van Wijk et al., 2003). From a management perspective, catch data alone may not reflect the sex composition in macrourid stocks, potentially increasing vulnerability to fishing.

4.5 | Size patterns

In terms of mean size, *M. holotrachys* was consistently larger, *M. carinatus* and *M. caml* were intermediate and *M. whitsoni* was the smallest species with a narrower size range. Despite these differences, the four macrourid species displayed similar length-weight relationships, suggesting analogous growth patterns (Figure S8). Apart from *M. whitsoni*, the recorded lengths and weights align with values reported in sub-Antarctic and Antarctic waters, although there is

some geographic variation (Dell et al., 2015; Laptikhovskiy, 2011; Moore et al., 2022; Morley et al., 2004; Morley & Belchier, 2002; Pinkerton et al., 2015).

In three of the four studied macrourid species, females were consistently larger than males, though the degree of sexual dimorphism varied among species, being largest in *M. holotrachys* and *M. caml*, and lowest in *M. whitsoni*. Such female-biased size is well documented among Macrouridae (including for *M. whitsoni*, although not recorded at South Georgia) and gadoids in general (Bergstad et al., 2021; Laptikhovskiy, 2005; Lee et al., 2019; Marriott et al., 2006; Moore et al., 2022). The observed sex-size variation may reflect several mechanisms: (i) niche partitioning or reduced intraspecific competition, allowing the larger sex to exploit different prey or habitats (Moore et al., 2022; Ward et al., 2006); (ii) greater reproductive investment, as increased body size in females is often linked to higher fecundity (Laptikhovskiy, 2011; Marshall et al., 2022; Moore et al., 2022); and (iii) predation risk, whereby the larger sex monopolises resource-rich areas, and the smaller sex selects safer habitats to minimise predation (Wearmouth & Sims, 2008). Consequently, sexual size dimorphism is closely tied to the observed pattern in size with depth and to the skewed sex ratios in the catches (see Section 4.4).

The bigger-deeper trend is well documented among deep-sea fishes, including macrourids (Collins et al., 2005; Dell et al., 2015; Eastman, 2017; Marriott et al., 2006; Murua, 2003). The exceptions stem from small sample sizes or shallower survey depths (< 1000 m), thus missing the full adult size range (Morley et al., 2004; van Wijk et al., 2003). These surveys in van Wijk et al. (2003) and Morley et al. (2004) corroborate this pattern as most individuals sampled were < 40 cm TL, a size class rarely caught by longline fisheries (Pinkerton et al., 2012; Dell et al., 2015, this study). However, not capturing smaller individuals in longline fisheries may also be due to size selectivity associated with the large hook size.

The general size-depth relationship was supported by our results, particularly for *M. holotrachys* and *M. caml*, in which larger individuals (mostly females) occupied deeper waters. By contrast, there was no clear size-depth trend in *M. whitsoni* at South Georgia, and the fish were smaller than those reported at higher latitudes such as the Ross Sea (Marriott et al., 2006; McMillan et al., 2012; Moore et al., 2022; Pinkerton et al., 2015). Local habitat conditions or interspecific competition may thus constrain *M. whitsoni* size at South Georgia, as in the northern South Sandwich Islands (Fitzcharles, 2014; Queirós, 2024). Further research exploring latitudinal size variation across the South Sandwich Islands archipelago would help clarify these discrepancies (Hollyman et al., 2022).

Size-depth relationships can also influence feeding ecology, including a greater reliance on scavenging by adults at greater depths (Collins et al., 2005; Pinkerton et al., 2013; Queirós et al., 2025), which may make them more susceptible to baited hooks. Larger individuals of *M. holotrachys* and *M. caml* may exploit different prey resources than their smaller or shallower conspecifics (Fitzcharles, 2014; Moore et al., 2022; Pinkerton et al., 2012; Pinkerton et al., 2013; Queirós et al., 2025). Knowledge of the diet and movement patterns is thus essential for

understanding how size variation shapes ecological roles within *Macrourus* populations.

From a management perspective, understanding species-specific size distributions and depth preferences is critical. Catching larger females can disproportionately reduce the reproductive capacity of a population, potentially causing a decline, although predation release may partially offset this effect (Grüss et al., 2023; New Zealand Ministry for Primary Industries, 2024; Queirós et al., 2022). In particular, *M. holotrachys* may be at higher risk, as most of the fishing effort is concentrated where larger females predominate.

4.6 | Management considerations

Understanding how longline operations affect individual *Macrourus* species is essential for establishing by-catch limits and efficiently manage fisheries following an ecosystem-based approach (Hollyman et al., 2022; Moore et al., 2022; Grüss et al., 2023; Trathan, 2023). Currently, no formal stock assessments exist for macrourids at South Georgia. The practice of reporting aggregated catches at the genus level is inadequate and should be phased out. Based on our results, we recommend the following improvements in data collection:

- i. Species-specific data: Encourage or require observers to identify *Macrourus* by-catch to species level whenever possible, using updated identification guides and additional training. This step would substantially improve the accuracy of by-catch reporting, enabling more robust assessments of status.
- ii. Observer training: Organise regular workshops for observers to refine macrourid identification, sampling protocols and data recording best practices. Empowering observers with up-to-date knowledge should ensure higher-quality data collection.
- iii. Improved sampling: Representative sampling of each line should be a requirement, rather than recording only the first five macrourids. This could be based on both increased sampling and randomising the sections of the line that are sampled, rather than focusing on initial or final segments, which would reduce bias and ensure that smaller or less-abundant species are recorded more consistently.
- iv. Expanded temporal and spatial coverage: Supplement fishery data with potential scientific surveys, particularly in underexplored shallower (< 700 m) habitats, to capture life-history stages not commonly sampled (e.g., juveniles in shallower waters) and refine habitat models and biological parameters (i.e., growth rates, age at maturity).
- v. Further ecological and biological data: Determine age, diet, trophic ecology, reproductive biology and migratory patterns for each *Macrourus* species to clarify how ecological factors influence their vulnerability to fishing.

5 | CONCLUSION

Our results demonstrate that aggregating *Macrourus* by-catch data at the genus level obscures critical differences in distribution, life-history

traits and vulnerability between the species (i.e., *M. caml*, *M. carinatus*, *M. holotrachys* and *M. whitsoni*) by-caught in toothfish fisheries at South Georgia (CCAMLR subarea 48.3). The framework applied here, as well as most of the management considerations, are easily transferable to other longline and trawl fisheries where by-catch is still reported in aggregate or with insufficient taxonomic detail. Treating target-species status as a proxy for the condition of the wider fishery is a common error, as non-target taxa can often follow distinct trajectories. Here, this is mainly concerning for *M. holotrachys*, which had a wide distribution and high catch rates. Our results also indicate a clear need to monitor sex ratios at key depths, given the implications of the strong female bias in catch rates for stock productivity. By contrast, *M. carinatus* and *M. whitsoni* exhibited more localised or depth-specific distributions, reinforcing the value of species-specific insights for effective by-catch management. Species-level information is critical for improving management and estimating specific by-catch thresholds (McMillan et al., 2012). Our results for *Macrourus* species at South Georgia represent a major advance towards those objectives.

AUTHOR CONTRIBUTIONS

José Abreu: conceptualization, writing – original draft preparation, data curation, methodology, formal analysis, funding acquisition, visualization, writing – review and editing. **Philip R. Hollyman:** conceptualization, writing – original draft preparation, methodology, data curation, supervision, writing – review and editing. **Jennifer F. Freer:** methodology, formal analysis, visualization, writing – review and editing. **M. L. Romero Martínez:** validation, writing – review and editing. **José P. Queirós:** methodology, writing – review and editing. **Timothy Jones:** methodology, writing – review and editing. **Richard A. Phillips:** conceptualization, writing – original draft preparation, supervision, writing – review and editing. **José C. Xavier:** conceptualization, supervision, funding acquisition, writing – review and editing. **Martin A. Collins:** conceptualization, writing – original draft preparation, methodology, data curation, supervision, writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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