

Full length article

Trends in population structure of Patagonian toothfish over 25 years of fishery exploitation at South Georgia

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ABSTRACT

Patagonian toothfish (*Dissostichus eleginoides*) supports valuable fisheries across the Southern Ocean under the management of the Commission for the Conservation of Antarctic Marine Living Resources. The fishery at South Georgia accounts for 26 % of the catch of this species in the Southern Ocean in the last 25 years. This study assesses the effects of exploitation and changes in management of the fishery on long-term trends in biological traits of Patagonian toothfish at South Georgia. Our results show variability in the size of fish, but no evidence of a systematic decline during the 25-year period. The mean size of fish was linked to recruitment, with pulses of recruitment associated with a reduction in mean size of the fishery. The years when recruitment was highest were in 2000–2010, with >50 % of toothfish of length classes < 90 cm. Management measures implemented over the last 25 years, including depth restrictions and benthic closed areas, have resulted in a gradual stabilization of the population structure. Catch per unit effort (CPUE) dropped from 1997 to 2010, gradually increased until 2017 and since 2018 has returned to values typical of the mid-2010s. Monthly changes in fish length, depth of capture and CPUE confirm that the spawning peak is in July. Size at maturity has remained stable over the last 25 years, suggesting the fishery has not had a major impact on population size structure. These results illustrate the role of management regulations in limiting the impacts of commercial exploitation on the population structure of a long-lived fish species. Given the bigger-deeper size pattern in Patagonian toothfish, there may be a case for increasing the minimum depth of the fishery (currently 700 m) when strong recruitment pulses are detected.

1. Introduction

The socio-economic importance of capture (wild) fisheries is expected to increase in the coming decade (United Nations, 2015; Gattuso et al., 2018; FAO, 2020). The number of stocks exploited at an unsustainable level has increased from 10 % in the 1970s to 34 % in 2017 (FAO, 2020). Currently, fisheries capture more than 90 million tonnes of fish per year, not accounting for the significant quantities of unwanted fish discarded at sea, as well as the catch from Illegal, Unregulated and Unreported (IUU) fishing (Zeller et al., 2018). Due to the lack of essential knowledge of the biology and ecology of target species, scientific advice to improve sustainability has frequently lagged behind the development and exploitation of fisheries (Morato et al., 2006; Bailey et al., 2009; Brooks et al., 2018). This is despite studies which highlight the key role

of fisheries as a driver of population dynamics of exploited fish (Hollyman et al., 2021; Subramaniam et al., 2022).

The primary impact of fishing is the reduction in abundance of the target species, which can lead to overexploitation (Pauly et al., 2002; Hilborn et al., 2020). The most well-known cases are the fisheries for Atlantic cod (*Gadus morhua*) and orange roughy (*Hoplostethus atlanticus*), in the 1962–1992 and 1978–2003 periods respectively, which resulted in population collapses, due to a poor understanding of fish biology and life history (Hutchings and Myers, 1994; Hilborn et al., 2006). These collapses had severe negative repercussions for both ecosystems and economies (Hutchings and Myers, 1994; Crespo and Dunn, 2017).

A second direct impact of fishing is that it may drive and select for specific life-history traits (e.g., size at maturity, fecundity, reproductive biology, distribution, diet) that vary with body length (Rochet, 1998;

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Blanchard et al., 2005; Péron et al., 2016). Size structure plays an important role in maintaining reproductive potential and stability of fish populations, as size is usually a major determinant of metabolic rate and energy allocation to growth, reproduction and foraging (Chung et al., 2019; Alencar et al., 2022). Accordingly, older and larger individuals contribute more to the reproductive output of a population, as they tend to produce more eggs, potentially extending the spawning period and enhancing recruitment (Morato et al., 2006; Anderson et al., 2008; Wright and Trippel, 2009). Thus, a well-balanced size-structure may provide more capacity to sustain a population if conditions are unfavourable (Schindler et al., 2010; Ruiz-Díaz et al., 2022). However, when fishing pressure selects for older and larger individuals, this can lead to truncation in the size structure of the population. Removal of larger fish can therefore lead to the relaxation of intraspecific competition for available resources, which may accelerate the growth of those fish that remain (Morato et al., 2006; Sharpe and Hendry, 2009). This may result in changes in size at maturity of the population (Olsen et al., 2004; Tu et al., 2018). Hence, from a biological as well as an economic perspective, it is essential to monitor changes in size structure in exploited fish populations (Grilly et al., 2015; Hilborn, 2020).

The Southern Ocean is one of the world’s largest fishing areas, where demand is expected to grow (Trathan et al., 2014; Brooks et al., 2016). Concerns about overexploitation of marine resources led to the

establishment of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR, a dual conservation and management body) in 1982. CCAMLR, which is part of the Antarctic Treaty System, is responsible for the conservation and management of marine resources, and aims to apply precautionary, ecosystem-based approaches to minimize the impacts of fisheries on target and non-target species, as well as on the ecosystem as a whole (Constable et al., 2000; 2011; Hanchet et al., 2015). CCAMLR regulates all fishing activities through a suite of annually agreed Conservation Measures (CMs) which apply broadly to the waters south of the Antarctic Polar Front (Constable et al., 2000; Collins et al., 2021). Within this area there are some regions under national jurisdiction, such as South Georgia in CCAMLR sub-area 48.3 in the southwest Atlantic Ocean (Fig. 2), in which additional domestic measures may apply.

The Patagonian toothfish (*Dissostichus eleginoides*) is a large (maximum >2 m, >150 kg), long-lived predator and scavenger that is distributed around many sub-Antarctic islands and off the South American coast, and is exploited both inside and outside CCAMLR waters (Collins et al., 2010). Following initial rapid growth in shallow shelf waters (Collins et al., 2007), Patagonian toothfish undertake an ontogenetic migration into deeper water (>500 m) where adults grow relatively slowly, mature late and have a life span exceeding 40 years (Collins et al., 2010). The spawning period is between April and

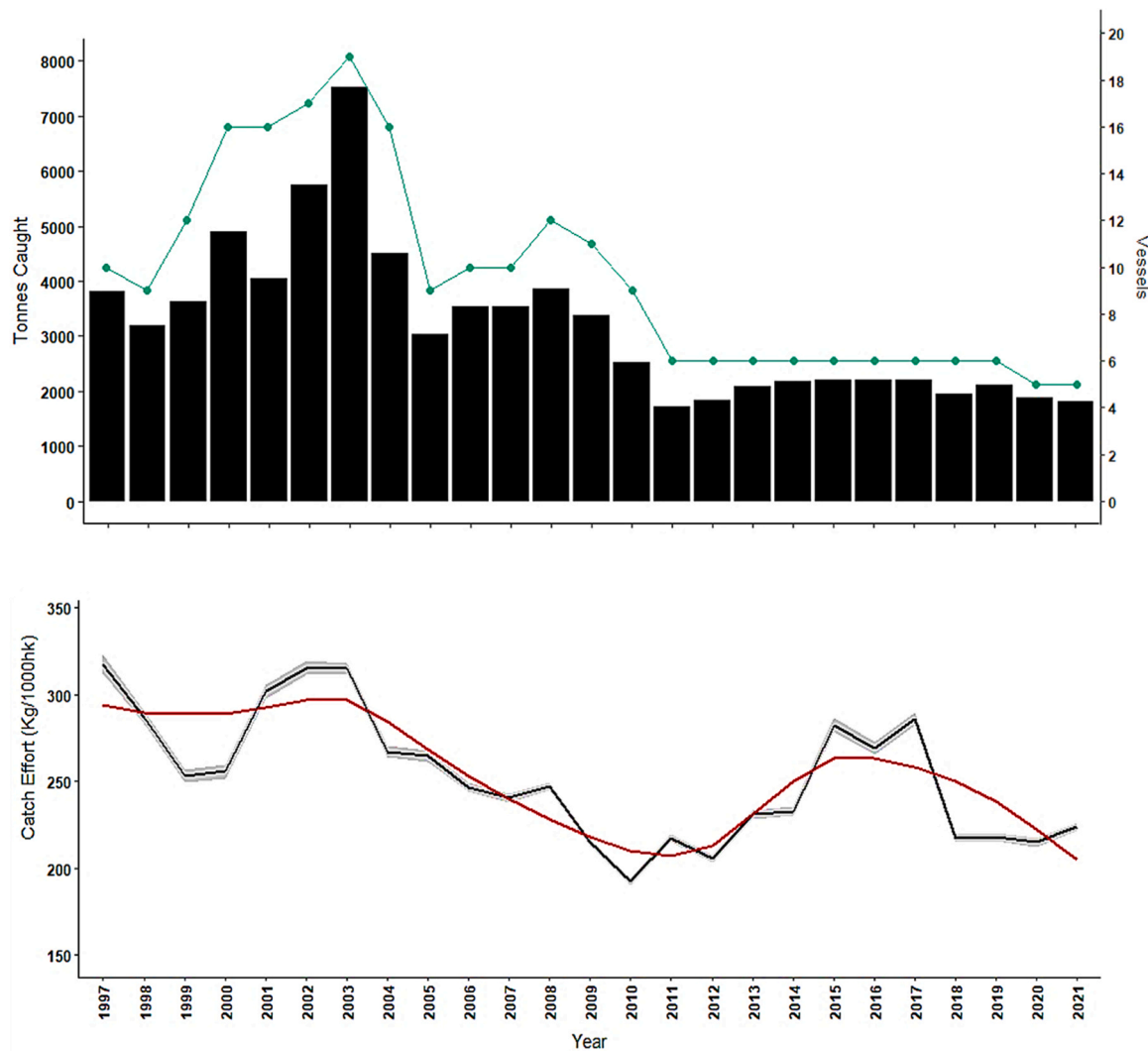


Fig. 1. Summary of the total catch of Patagonian toothfish in the longline fishery at South Georgia (CCAMLR area 48.3), from 1997 to 2021. Top panel: left axis and black bars shows the reported tonnes caught; right-axis and coloured line shows the number of recorded vessels fishing in each year. Lower panel: fitted catch per effort (CPUE: kg per 1000⁻¹ hooks) of the 25-year time series, resulted from the GLM. Loess smooth added to the plot. Grey shading indicates confidence interval.

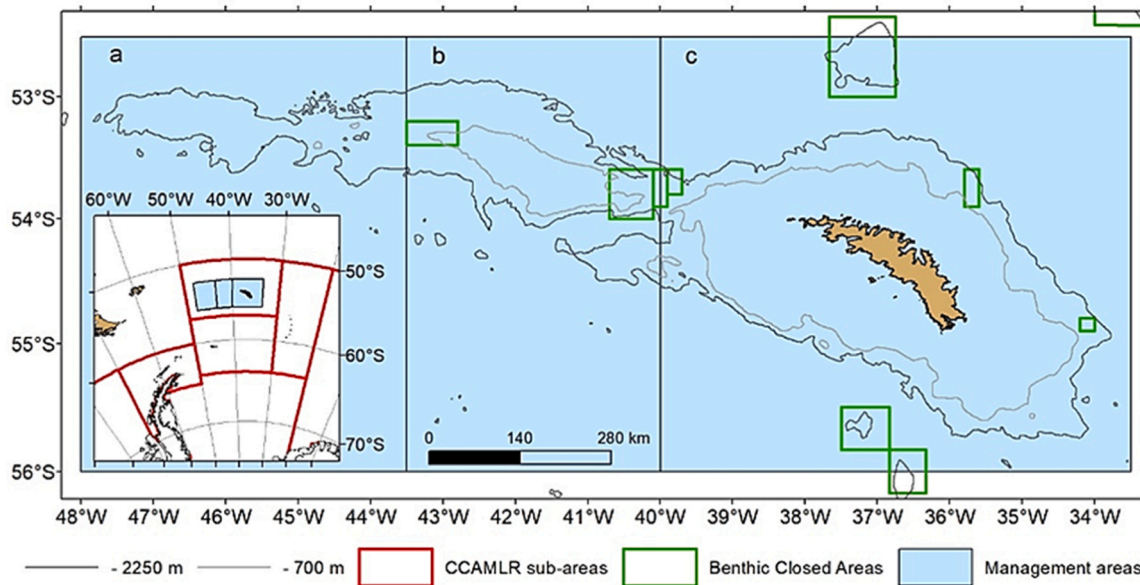


Fig. 2. Map of South Georgia (Management Area C) and Shag Rocks (Management Area B), CCAMLR sub-area 48.3. The inset highlights the area of interest in the Southwest Atlantic Ocean. The contour lines reflect the depth restrictions currently implemented (light grey – 700 m; dark grey – 2250 m).

September, with a peak in July (Agnew et al., 1999; Brigden et al., 2017; Bamford et al., 2024).

The Patagonian toothfish is currently the most valuable target species in the Southern Ocean (Rogers et al., 2015; Reid, 2018) and Patagonian toothfish catches at South Georgia represent 25.7 % (Table S1) of the total catch of this species in the Southern Ocean over the last 25 years. Besides its economic importance, toothfish also perform an important ecological role, as a predator of fish, cephalopods and crustaceans, and as prey for marine mammals, such as sperm whales (*Physeter macrocephalus*) and seals (Collins et al., 2010; Roberts et al., 2011; Troccoli et al., 2020).

Fishery data have been systematically collected since 1997 by CCAMLR registered scientific observers. This has provided a suite of information on Patagonian toothfish at South Georgia over an extended period, used mainly to perform stock assessments (CCAMLR, 1995, 2019). Although there are some studies on the ecology and biology of toothfish (Collins et al., 2007, 2010; Brigden et al., 2017), there are still gaps in our knowledge of their life history and responses to fishing pressure. In particular, some studies suggest fishing has changed the size-age structure, based on analyses of restricted time series (Shust and Kozlov, 2006), or the reproductive traits and length of fish caught (Brigden et al., 2017).

Deep-sea fish such as Patagonian toothfish, are generally more vulnerable to exploitation than fish on continental shelves (Laptikhovskiy and Brickle, 2005). As such, deep-sea fisheries require stricter adherence to precautionary principles to avoid overexploitation and potential stock collapse. Indeed, the application of the precautionary approach (implemented by CCAMLR) is a key element in trying to ensure sustainable fisheries management and requires that gaps be filled in terms of knowledge of the target stock and long-term impacts of fishing (Constable, 2011; Chown and Brooks, 2019).

Within this context, our study evaluated the long-term effects of the longline fishery on the Patagonian toothfish population in South Georgia waters from 1997 – 2021. Specifically, our aims were to: i) evaluate how the population structure of Patagonian toothfish has changed from the early years of the fishery to the present, ii) understand the effectiveness of specific changes in fisheries regulation and iii) identify possible management actions to better ensure the sustainability of the longline fishery into the future.

2. Methods

2.1. Data collection

Data were obtained from the CCAMLR Secretariat on the catches of Patagonian toothfish by the commercial longline fishery at South Georgia (CCAMLR area 48.3; vessel catch reports), from 1997 to 2021. These included the number of sets/hauls, number of hooks set, date, latitude, longitude, and depth (m). Although the fishery started in the late 1980s, and scientific observers were first deployed in 1994, systematic observer data from all vessels are only available from 1997 onwards.

The toothfish fishery at South Georgia is a demersal longline fishery, which involves the setting of longlines of around 10 km in length, that sink to the seafloor. There are two main gear systems, *spanish* (or double line) and *autoline*; both gears are attached at each end to an anchor and buoy line, but *spanish* gear comprises a strong main line from which a series of connecting weighted ropes are attached to the fishing line, whereas *autoline* gear is a single weighted line (Collins et al., 2010). In both systems, hooks are attached by short lengths of line (snoods) to the fishing line. Consequently, the hooks of *spanish* lines may fish further above the seafloor than those on *autolines*. After a typical soak period of 6–48 hours, the line is hauled on board. Most vessels used *spanish* gear until 2006, and thereafter there was a general trend towards greater use of *autoline* gear (Table S2). Given the operational differences, gear type was included as a factor in relevant analyses.

Since 1995, the toothfish fishery at South Georgia has been restricted to the austral winter to minimise the incidental mortality (bycatch) of seabirds (Collins et al., 2021). However, there were some exceptions in early years (Table S2). Fishing occurs on the South Georgia and Shag Rocks shelf-break areas, which are separated by a deep channel (~1500 m; Fig. 2); for some analyses these two regions were considered separately. Observers on board each vessel select a sub-sample of hauls on an ad-hoc basis to fit with working patterns and record biometrics of the catch. These include the number of individual toothfish and various parameters (total length in cm, sex, maturity stage, weight in kg). These observations were made in accordance with the CCAMLR Scheme of International Scientific Observation (CCAMLR, 2020). Data were submitted to CCAMLR and are jointly owned by the observer designating and fishing Members. Unless stated, all statistical analyses were

conducted within the R environment v. 4.0.3.

2.2. Fish biometrics

Long-term changes in total length (TL) (hereafter length), sex ratio, condition (K), size at maturity and catch per unit effort (CPUE) of the Patagonian toothfish were considered in relation to the conservation measures and restrictions introduced to the fishery during the study period (Table 1). To ensure comparisons across years were like-with-like, analyses were restricted to data collected: (i) from 1st April to 31st August; (ii) from > 700 m (in accordance with the depth restriction introduced in 2011), based on the midpoint between the initial and final depths recorded for the set; (iii) outside the boundaries of the Benthic Closed Areas and iv) from management areas B and C (Fig. 2). Any records involving obvious typographic, or transcription errors were also removed. A summary of the filtered dataset is provided in Table S2. Observer data from most or all vessels in the fishery each year were available from 1997 to 2021, which included data from 230 of the 240 vessel/season combinations. Due to sex differences in growth rate and size at maturity in Patagonian toothfish, analyses were conducted separately for males and females.

Generalised linear models (GLM) were fitted for each sex using a gaussian error structure with log-transformed length as the response variable. Independent variables, year and depth were continuous, and month, region and gear were included as factors. We used the “performance” R package (Lüdecke et al., 2021) to evaluate model assumptions, including linearity, homogeneity of variances, collinearity (evaluated using the variance inflation factor, with values < 2, assumed not to have an effect on model), normality of residuals and performance (Akaike’s information criterion or AIC). Results are reported as mean ± standard deviation unless otherwise stated. Differences were considered statistically significant at $p \leq 0.05$. Possible changes in length frequencies were also examined based on five-year bins, and length-depth relationships were also explored separately for each sex.

To calculate the size at maturity, the CCAMLR catch data from the commercial fishery were supplemented by data on juvenile Patagonian toothfish obtained from bottom trawl surveys on the South Georgia & Shag Rocks shelves between 1997 and 2019 (for details, see Hollyman et al., 2021). The data were grouped into five-year periods and 1 cm length bins, and only bins containing ≥ 5 individuals were used in further analyses. Preliminary analyses confirmed that the inclusion of

Table 1

Key events and Conservation Measures applied since the beginning of the longline fishery of Patagonian toothfish at South Georgia.

Year	Key Events and Conservation Measures
1988	Beginning of longline Patagonian toothfish fishery.
1991	CCAMLR implements the first catch limit.
1994	CCAMLR define 48.3 as Special area for Protection and Scientific study. Inclusion of Scientific Observer.
1995	Season period restriction (winter months). Night setting only.
1996	Direct fishing only allowed by longline.
1998	First mention to bycatch species. Biological data required.
2001	Bycatch limits for grenadiers, skates and rays. All toothfish caught count against the total allowable catch even when discarded.
2002	Dumping offal prohibited during set and avoided during haul.
2004	Minimum depth of 500 m introduced.
2005	Fishing area restricted and divided into 3 management areas (A, B & C), with 10 tonne catch limit in Area A.
2006	Area A closed (catch limit of 0).
2008	Benthic Closed Areas introduced.
2010	Minimum fishing depth increases to 550 m.
2011	Minimum fishing depth increased to 700 m.
2012	Longline fishing restricted to depths between 700 m and 2250 m. Benthic Closed Areas refined.

the data from the groundfish surveys did not alter the shape of curves fitted to the data from the commercial fishery. Maturity stages followed the classification in Kock, Kellermann, (1991); stages 1–2 were considered to be immature, and stages 3–5 to be mature (for more details, see Bamford et al., 2024). Size at maturity calculations were made using logistic regression in the sizeMAT package in R (Torrejon-Magallanes, 2019).

A relative body condition factor (K) for each fish was calculated using the Fulton Index as a proxy for physiological status, according to the following equation: $K=100(W/TL^3)$, where W represents total weight and TL is the total length. This length-weight relationship has been validated for various fish species (Shin et al., 2005). Values are distributed around 1, with values above 1 representing individuals in better condition than average, and values below one, representing individuals in worse condition. We assumed that the effect of stomach fullness on values were negligible across years due to the very large sample sizes (Table S2).

2.3. Catch per unit of effort (CPUE)

Catch per unit effort (CPUE, kg per/ 1000⁻¹ hooks) was calculated for each longline. To ensure comparisons across years were consistent, data followed the same restrictions used for the fish biometrics. Temporal changes in CPUE over the study period were analysed by fitting a negative binomial GLM and log link function, through R package “MASS”, where the response variable was the CPUE and explanatory variables were area (here divided between South Georgia and Shag Rock islands, see Fig. 2), year, depth, month (April to August), and gear type (autoline and spanish).

3. Results

3.1. Population structure

Based on a sample of 285,824 individual Patagonian toothfish (154,241 females and 131,583 males), a higher proportion of females (54 %) than males (46 %), both overall and within years, were caught in the longline fishery at South Georgia (Table S2), from 1997 to 2021. The sex ratio differed between months, with an increase in the proportion of females (to ~ 60 %) in July and August.

The mean length of fish varied between years (Fig. 3A), with similar patterns for both males and females. Overall, the mean length of both male and female fish declined from 1997 (F: 100.5 cm; M: 91.65 cm) to 2001 (F: 89.9 cm; M: 84.7 cm), was broadly stable for several years, and then in 2012 dropped to the lowest values recorded (F: 87.4 cm; M: 82.7 cm). From 2012 onwards, the mean length increased gradually, with values in 2021 (F: 97.7 cm; M: 90.3 cm) similar to those in 1998. In the 25-year study, the largest recorded female and male were 247 cm (~1300 m depth) and 183 cm (~1000 m depth), caught in 2009 and 2000, respectively.

The proportion of smaller fish in catches (< 90 cm TL or 80 cm TL), which is likely to be indicative of the recruitment, also fluctuated considerably among years (Fig. 3C). There were lower proportions of small fish in the early years of the fishery, increasing to 50–65 % (< 90 cm TL) and 20–30 % (< 80 cm TL) of the catch between 2001 and 2010. The highest proportions of small fish were in 2009–2012, which indicates a period of good recruitment to the fishery (Fig. 3C). Since 2013 there has been a gradual drop in the proportion of small fish, with the lowest % of fish < 80 cm in 2021. The fishery operated at shallower depths on average in the early years but has been stable at mean of ~ 1300 m since 2001 (Fig. 3B).

There were positive relationships between both year and depth, and body length (TL) of male and female toothfish over the 25-year study (Table 2). Month was also a significant factor, with larger fish caught in April than in May to August. The greatest difference in mean fish lengths for females was between April and May, whereas the smallest, male fish

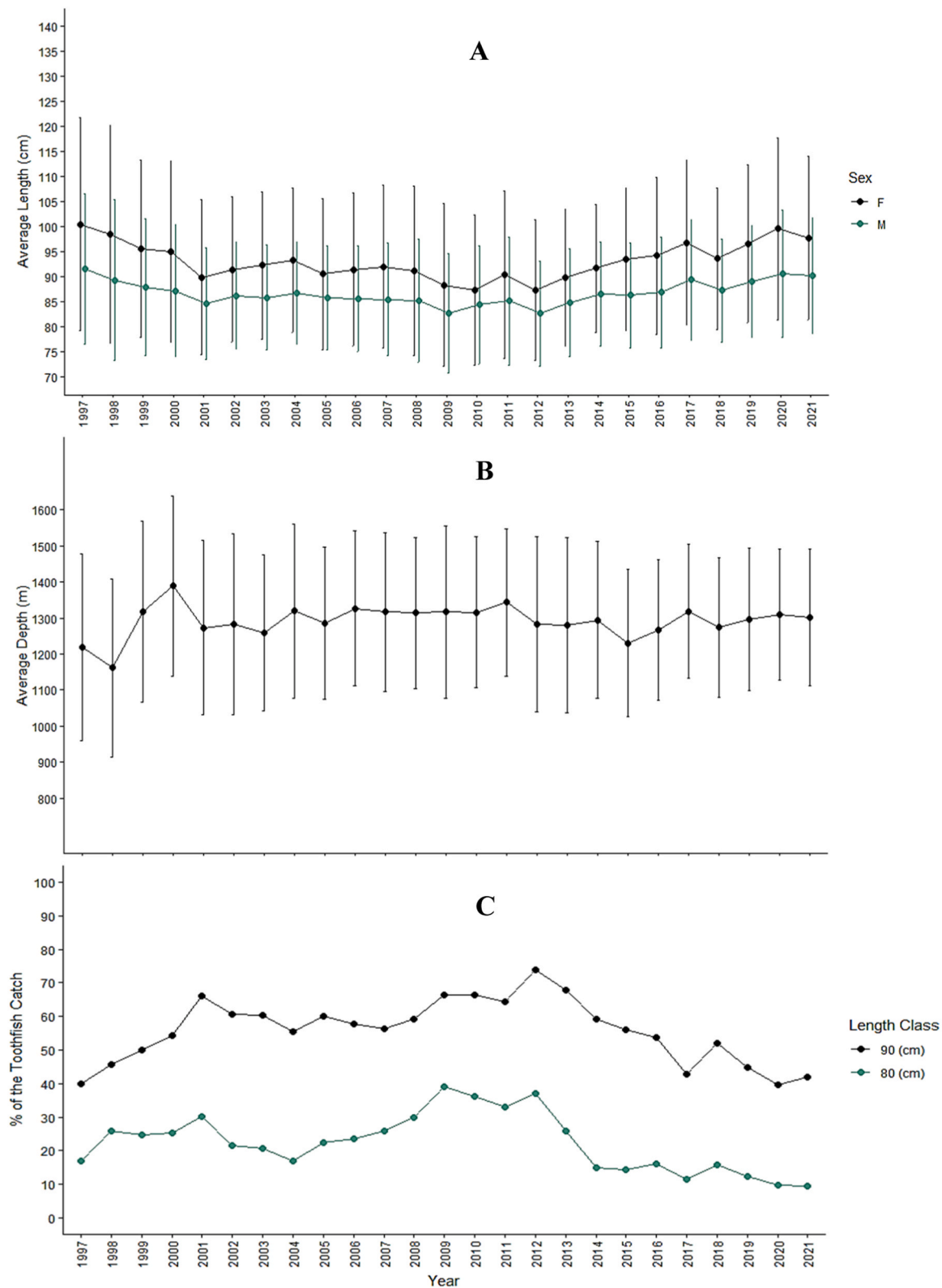


Fig. 3. Annual changes in the characteristics of Patagonian toothfish catches in the longline fishery at South Georgia (CCAMLR area 48.3), from 1997 to 2021, (A) average length \pm SD of male and female toothfish caught. Black line is female (F), green line is males (M); (B) average depth \pm SD of fishing sets; (C) percentage of small toothfish size classes (young fish) in the total catch. Black line, individuals below 90 cm TL, green line, individuals below 80 cm TL.

were caught in July. Mean fish length was greater at Shag Rocks than at South Georgia, particularly for males. Lastly, mean lengths were greater for fish caught in *spanish* than *autoline* gear for both sexes (Table 2). This difference between *spanish* and *autoline* gear was also verified for the

period where there was an equal number of vessels operating each gear, giving a similar outcome.

Monthly patterns in frequency distributions of TL (Fig. 4), confirm the results of the GLMs for both sexes (Table 2). The violin plots showed

Table 2

Results of generalised linear models for female and male Patagonian toothfish between 1997 and 2021. Body length was the response variable. April, South Georgia and *Autoline* are the base case in each respective factor. SR – Shag Rocks. Female sample n = 154,241; male sample n = 131,583.

Coefficient	Estimate	St. Error	t-value	P value	Deviance				
					Residual	df	Null	df	
Females	Intercept	0.561	0.141	3.971	<0.001	4040	154232	4169	154240
	Year	0.002	0.000	26.927	<0.001				
	Depth	0.003	0.000	62.461	<0.001				
	May	-0.014	0.002	-7.303	<0.001				
	June	-0.006	0.002	-3.174	0.002				
	July	-0.009	0.002	-4.512	<0.001				
	August	0.004	0.002	1.906	0.057				
	Region ~ SR	0.005	0.001	4.568	<0.001				
	Gear ~ <i>spanish</i>	0.023	0.001	23.628	<0.001				
	AIC = -124035								
Males	Intercept	1.219	0.126	9.690	<0.001	2182	131574	2255	131582
	Year	0.002	0.000	24.736	<0.001				
	Depth	0.000	0.000	57.032	<0.001				
	May	-0.007	0.002	-4.241	<0.001				
	June	-0.005	0.002	-2.993	0.003				
	July	-0.017	0.002	-10.279	<0.001				
	August	-0.007	0.002	-3.932	<0.001				
	Region ~ SR	0.018	0.001	20.186	<0.001				
	Gear ~ <i>spanish</i>	0.018	0.001	21.399	<0.001				
	AIC = -165970								

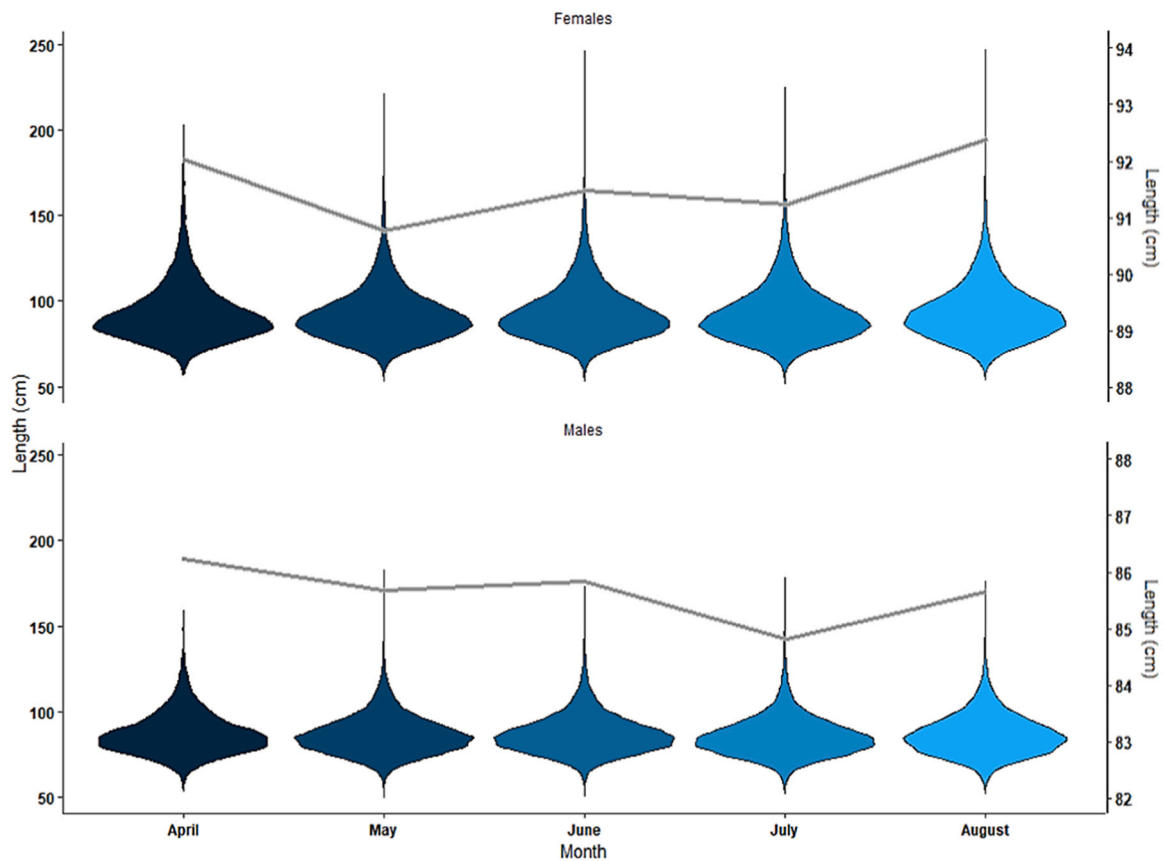


Fig. 4. Violin plots of body lengths of female and male Patagonian toothfish (left-axis), for each month (April to August) of the fishing season. All years represented. Gray line is the month effect on toothfish length, from the generalised linear model (Table 2) (right-axis).

limited variability probably because the effect of month in the GLM was small, albeit statistically significant (Fig. 4). There was a positive relationship between depth and body length of both sexes, with a greater range of lengths independent of depth in females than males (Fig. 5), and at 1300–1400 m, where a considerable portion of the fishing occurs (Fig. 3B). The average TL was 87.8 cm and 83.0 cm for females and males, respectively, at the lowest depth (700–800 m), 100 cm and

90.3 cm at greater depths (>1800 m), and 91.7 cm and 86.0 cm between 1200 and 1300 m, where most of the toothfish are caught.

3.2. Size at maturity and body condition

Of the 154,241 female toothfish caught over the 25 years, 69 % were immature (stage 1 and 2) and 31 % were mature (stage 3, 4 and 5). By

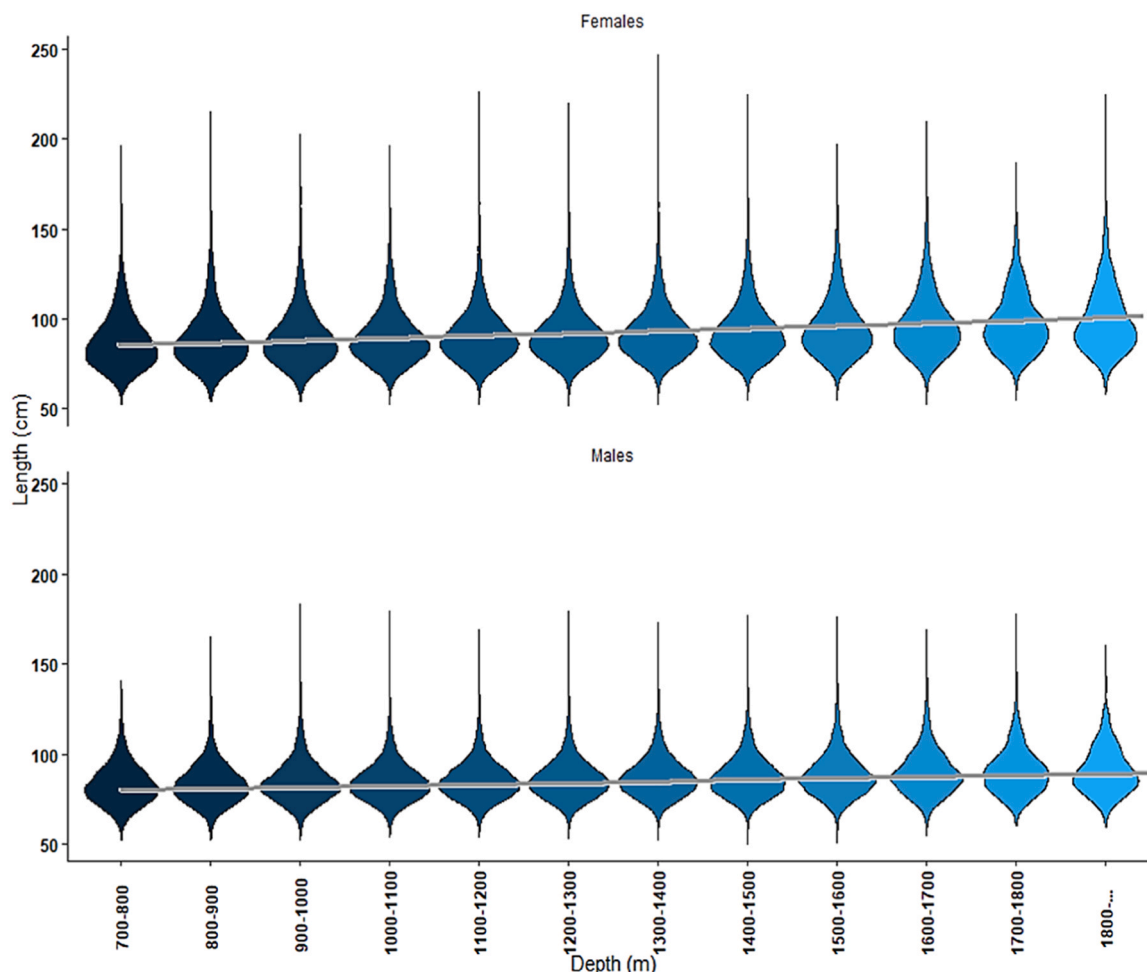


Fig. 5. Violin plots of lengths of female and male Patagonian toothfish by depth bin in the longline fishery. All years represented. Gray line is the depth effect on toothfish length from the generalised linear model (Table 2).

comparison, of the 131,583 males, 28 % were immature and 72 % mature. The contribution of immature toothfish (both females and males) peaked during the period from 2010 to 2013, indicative of strong recruitment (Fig. 3C). The fishery changed during the study period in terms of depth limits, spatial closures, and the ratio of *spanish:autoline* vessels.

Based on comparisons between 5-year bins (corresponding to changes in management measures; Table 1), there was a clear difference in the size that sexes reach maturity, which was between 100 and 110 cm TL in females, and between 70 and 80 cm TL in males (Table 3). The clearest difference between periods were in males, with a 6 % decrease in the size that they reach maturity from the first to last 5-year period over the 25-year study, with the greatest change from the first to second period (1997 – 2001–2002 – 2006). In contrast, the size at maturity was more consistent in females, with the difference between the first and last 5-year periods being less than < 1 %.

Based on Fulton’s K factor, male and female Patagonian toothfish at South Georgia were in good body condition, with a mean K = 0.98, for all years, and little variation in the mean among 5-year periods (Table S4). There were no major differences in body condition between months in either sex, other than a slight drop in condition of males during August to K=0.94 (Table S4). There was a gradual increase in male condition from stage I (K=0.95) to stage III (K=0.99), and then a decrease by stage V (K=0.94). Females followed a similar pattern, with body condition increasing from stage I (K=0.95) to stage IV (K=1.05), then dropping in stage V (K=0.97).

Table 3
Size at maturity of female and male Patagonian toothfish, in each 5-year period at South Georgia and the respective magnitude of change from the base period.

Sex	Period	Size at Maturity (cm)	Confidence Limits	Magnitude of change (%)	
				Between Periods	Initial & Final
Females	1997 – 2001	101.3	100.9 – 101.8		
	2002 – 2006	103.4	103.1 – 103.8	↑ 2 %	
	2007 – 2011	101.1	100.8 – 101.5	↓ 2 %	↓ < 1 %
	2012 – 2016	106.5	105.9 – 107	↑ 5 %	
	2017 – 2021	100.9	100.6 – 101.2	↓ 5 %	
	1997 – 2001	76.7	76.4 – 77.1		
Males	2002 – 2006	73	72.7 – 73.4	↓ 5 %	
	2007 – 2011	73.5	73.2 – 73.8	↑ 1 %	↓ 6 %
	2012 – 2016	74	73.4 – 74.5	↑ 1 %	
	2017 – 2021	72	71.1 – 72.8	↓ 3 %	

3.3. Catch per unit of effort

Over the 25-year study CPUE (sexes combined) initially decreased, and since then has fluctuated considerably among years, with peaks in 2001–2003, and 2015–2017 (Fig. 1). The peak in 2001–2003 coincided with both the highest catches and number of vessels operating in the fishery. The CPUE was lowest in 2010 and 2012, which corresponds to the introduction of stricter management measures (Table 1). The CPUE has been broadly stable since 2018.

The fluctuations in CPUE are consistent with the model output (Table 4). Depth, although significant, did not influence the overall CPUE, as the fishery has operated within the same range over the years. The highest CPUE by month was in April, after which the CPUE decreased until July, but then increased in August. The mean CPUE was higher at Shag Rocks than South Georgia, and for *spanish* than *autoline* gear.

4. Discussion

This study evaluated the impact of the longline fishery on Patagonian toothfish at South Georgia over a 25-year period (1997 – 2021). Although previous studies have addressed some of the issues explored here (Agnew et al., 1999; Everson and Murray, 1999; Shust and Kozlov, 2006; Brigden et al., 2017), these analysed only the early years of the fishery or a small portion of the extensive dataset that is now available and did not consider links with changes in regulations. We found no evidence of substantial changes in Patagonian toothfish population structure over the 25 years. Fisheries elsewhere have had major impacts on populations of long-lived target species (Hilborn et al., 2006; Morato et al., 2006), but our results suggest the careful regulation at South Georgia has been successful in reducing these effects.

Although the changes detected in the present study were small, suggesting a relatively stable population structure during the 25 years, it is important to note that exploitation of Patagonian toothfish in South Georgia started in 1988/89 (Collins et al., 2010). Considerable changes in the population could have occurred prior to 1997, particularly as the fishery was poorly regulated and there is uncertainty about catches by IUU vessels (Agnew, 2004; Collins et al., 2010). This likely reduced the proportion of larger and older fish before the start of our time series. However, it is now over two decades since there was evidence of substantial IUU fishing around South Georgia. It is also worth noting that the fishery operates in a narrow depth band, on a species with a distinct bigger-deeper trend (Collins et al., 2010; this study), so it is perhaps likely to catch a consistent size of fish.

Management of the fishery at South Georgia has evolved considerably over the years, with the implementation of a variety of regulations inside the fished area (Table 1). In particular, the introduction of Benthic Closed Areas was a major switch in space available for the fishery (Trathan et al., 2014). In addition, environmental conditions have changed around South Georgia for reasons unrelated to the longline fishery. Seals and whale numbers have increased rapidly since industrial

whaling ceased at South Georgia in 1965 (Trathan et al., 2014; Rogers et al., 2015; Bamford et al., 2022). Large scale oceanographic changes have been occurring in South Georgia, with higher sea surface temperatures and higher intensity of El-Niño events (Whitehouse et al., 2008). These may also have a role in determining toothfish population dynamics and biological traits. However, in general the effects of environmental conditions on long-lived benthic fish are likely most apparent during larval and juvenile phases (Lehodey et al., 2006). That may explain why we found little evidence of any consistent long-term trends in size structure or maturation patterns.

4.1. Population structure

Over the 25-year study, our analysis revealed a small, but consistent, difference in the sex ratio of Patagonian toothfish in the catch, with 2–20 % more females than males, as seen at other fishing grounds (Lord et al., 2006; Welsford et al., 2011; Péron et al., 2016). Within year, the bias in the sex ratio was least apparent in April and May but increased to ~ 60 % females in July and August. This could reflect sex differences in growth rates, as females grow more quickly and to larger sizes than males (Péron et al., 2016; Soeffker et al., 2022), and so may move sooner to deeper waters where the longline fishery operates (Fig. 3B). That would tie in with the high proportion (63 %) of males caught in July that are mature (larger), i.e., stage IV (Agnew et al., 1999; Brigden et al., 2017).

The largest females were caught in the fishery in April, and the smallest in May, whereas the smallest males were caught in July. Temporal changes in length are potentially linked to spawning behaviour (Agnew et al., 1999; Lord et al., 2006). At South Georgia, the peak in spawning is in July (Brigden et al., 2017; Bamford et al., 2024), with evidence of a secondary spawning period in April (Agnew et al., 1999; Bamford et al., 2024). There is also a decrease in CPUE in July (see explanation below) (Bamford et al., 2024; Collins et al., 2010). Such a change will primarily affect the larger mature fish, which may explain the reduction in mean length caught.

Previous studies suggested that both sexes may converge in intermediate depths to spawn (Agnew et al., 1999; Brown et al., 2013), in which case we would not expect a greater bias in the sex ration towards females in July and August. Hence, we suggest that during reproduction, there is a sexual spawning segregation, with males moving first for spawning grounds to shallower depths (< 1000 m), that are less targeted by the fishery (Fig. 3B), and so less likely to be caught, where they remain for longer time. Given the strong relationship between body length and water depth (Fig. 5), mature females which are more prevalent at deeper depths (Agnew et al., 1999), may move in and out to these spawning locations, potentially explaining the seasonal difference in the sex ratio of the catch.

Mean TL declined slightly in both male and female toothfish from 1997 to 2012, but then increased again such that the mean in 2021 was similar to values in the early years of the time series. The presence of larger fish in the early years was also seen during the development of the

Table 4

Results of the generalised linear models for Patagonian toothfish between 1997 and 2021. Catch per unit effort (CPUE: kg/1000 hooks) as the response variable. April, South Georgia and *Autoline* are the base case in each respective factor. SR – Shag Rocks.

Coefficient	Estimate	St. Error	Z value	P value	Deviance			
					Residual	df	Null	df
Intercept	25.04	0.398	62.859	<0.001				
Year	-0.010	0.000	-48.545	<0.001				
Depth	0.000	0.000	8.287	<0.001				
May	-0.188	0.005	-36.589	<0.001				
June	-0.305	0.005	-58.405	<0.001	303174	284469	330790	284477
July	-0.562	0.005	-106.200	<0.001				
August	-0.443	0.006	-80.027	<0.001				
Region ~ SR	0.018	0.003	6.242	<0.001				
Gear ~ <i>spanish</i>	0.105	0.003	39.077	<0.001				

Patagonian toothfish fisheries around Falklands, Kerguelen, and Heard Islands (Laptikhovskiy and Brickle, 2005; Duhamel et al., 2011; Ziegler and Welsford, 2017). The same pattern is seen in other fisheries worldwide (Birkeland and Dayton, 2005; Blanchard et al., 2005; Nogueira et al., 2015) where, at the onset of exploitation, populations are found closer to their pristine natural state and thus there is a wider size range, and more large individuals. Although the South Georgia longline fishery was poorly regulated prior to 1994, the fishery was operating mostly on the island shelf areas and was thus likely catching smaller individuals; however, from 1997 and 1998, there was a shift by vessels to the exploitation of deeper waters (Agnew, 2004).

Some truncation in the size distribution of an exploited population is inevitable, as seen in fisheries elsewhere (Blanchard et al., 2005; Shackell et al., 2010). At South Georgia, this likely took place in the early years of the fishery (1988 – 1996); that would explain why the mean length of fish caught since 1997 has been relatively stable, with periodic reductions likely associated with strong recruitment pulses when smaller, younger fish move to the depths exploited by the fishery (Belchier and Collins, 2008). This stability may also be due to greater regulation and consistency in areas and depths fished. There may also be a preference (price premium) for fish of an intermediate size, which are easier to package. Fishing at depths >1500 m, where some of the biggest individuals are caught, is more time consuming in terms of setting and hauling, even if the CPUE based on the number of hooks is similar.

From 1998 until 2012, mean toothfish length slowly decreased, due to the greater contribution of smaller size classes (<90 cm) to catches (Fig. 3C). There were some years between 2001 and 2012 when > 50 % of the catch was < 90 cm TL (Fig. 3C), leading to the concerns raised by Shust and Kozlov (2006) and Brigden et al. (2017) that there was a higher percentage of immature individuals in the catch and a decrease in average size of toothfish population. However, the increased representation of smaller fish is probably related to a strong cohort entering the exploited population. Recruitment of toothfish to the South Georgia stock is highly variable (Belchier and Collins, 2008; Collins et al., 2010), and may be linked to environmental variability. A very strong cohort was detected during groundfish surveys from 2003 (~ 20 cm) to 2008 (~ 65 cm) (Collins et al., 2010; Fig. 4.4) and probably appeared in fishery catches from 2009, when there was a clear increase in the proportion of small fish. It is likely that this cohort dominated the fishery for a few years, leading to a high proportion of relatively small fish until 2012. Further strong cohorts were reported in 2011 (Brown et al., 2011) and 2021 (Collins et al., 2021), but recruitment is likely to occur at lower levels in other years. In other commercial fisheries, average length of the catch has declined due to a strong recruitment year or cohort, which added smaller individuals to the population (Haedrich and Barnes, 1997; Nogueira et al., 2015).

From 2012–2021, mean length gradually increased, although there were some small fish seen in some years, these pulses of recruitment were likely weaker than those from 2002 cohort. A further pulse of recruitment was detected in the 2021 shelf trawl survey (~40 cm TL; Collins et al., 2021), but these will not yet be available to the fishery. It is also worth noting that the establishment of the Benthic Closed Areas, and the restriction of the fishery to depths greater than 700 m (see Table 1) were intended to reduce the capture of small fish. For consistency, our analysis excluded fish caught in the Benthic Closed Areas (during research lines for tagging) and shallower than 700 m. An analysis of the full data shows a similar pattern (Fig. S5).

Biological traits including length, size at maturity and spawning success, are sensitive to fishing impacts (Shin et al., 2005), but will also fluctuate in response to environmental and other factors, such as competition and predation pressure (Brooks et al., 2018; Hilborn et al., 2021). Mean toothfish body length increased significantly with depth for both females and males (Table 2, Fig. 5), and this pattern would be more distinct if we included catches from trawl surveys in shallower depths (Collins et al., 2007; 2010). This bigger-deeper pattern is also observed in Patagonian toothfish on the Patagonian shelf, and around Kerguelen

and Heard Islands, as well as for the Antarctic toothfish *Dissostichus mawsoni* (Laptikhovskiy et al., 2006; Welsford et al., 2011; Soeffker et al., 2022), and many other deep-sea scavenging fish (Collins et al., 2005). This trend is important for fishery management, as it allows measures to be in place to protect small fish. A minimum fishing depth of 500 m was introduced in 2004, increased to 550 m in 2010 and 700 m in 2011 (Table 1). Protecting small fish is essential as these will form the basis of future exploitation (Houde, 2012) and, when recruitment is highly variable, it is much more effective to protect small fish than try to protect spawning adults (Bamford et al., 2024). Slightly larger toothfish were caught around Shag Rocks, which could be due to higher productivity and prey availability in this region (Collins et al., 2007; Rogers et al., 2015). Hooks on the *spanish* gear are more likely to be above the seafloor when fishing (Benedet, 2017), which may explain the catch of larger fish. Hook and bait size may also be factors, but the size of hooks and bait were not always recorded in the early years. Whilst statistically significant, the influence of both region and gear type on toothfish length was negligible, yet important to keep in mind when monitoring possible trends.

4.2. Maturity and condition

In the long-term, there is evidence from a range of exploited species that higher adult mortality (both natural and from fisheries) selects for earlier maturity at smaller size, which causes a decrease in size at maturity (Beacham, 1983; Clark, Tracey, 1994; Lojo et al., 2022; and Table S3).

Our results indicate little change in Patagonian toothfish size at maturity over 25 years of exploitation. Previous studies in the Atlantic sector, including at South Georgia and the Patagonian Shelf (Everson and Murray, 1999; Collins et al., 2010; Soeffker et al., 2014) indicated that toothfish growth begins to slow around 78 cm TL, which equates to ~10 years of age and corresponds to the estimated age at first maturity. However, our findings show the pattern for females and males are different. Size at maturity of males has reduced (by ~6 %; Table 3), albeit within the range of values reported in past studies at South Georgia (Everson and Murray, 1999; Agnew et al., 1999). In contrast, there has been little change (< 1 %) in size at maturity of females (~101 cm TL). It appears that Patagonian toothfish in the Atlantic sector grow larger, and consequently attain a bigger size, and thus a bigger size at maturity than populations at Kerguelen in the Indian Ocean sector, where the average sizes at maturity are 63 cm and 85 cm TL for males and females, respectively (Lord et al., 2006). Differences in size at maturity could be unrelated to exploitation and instead be influenced by environmental conditions and/or productivity, due to the geographical and oceanographic settings, and population size, of the different regions (Péron et al., 2016; Bamford et al., 2024). Finally, it is worth noting that in females the mean size at capture was less than the size at 50 % maturity (Figure S3), whilst in males the mean size at capture was greater than size at 50 % maturity (Figure S4).

Trends in body condition can indicate a selective pressure, positive or negative, on a fish population, which may be caused by fishing or a change in habitat quality or environmental factors (Bolin et al., 2021; Soeffker et al., 2022). Both male and female Patagonian toothfish at South Georgia have maintained a stable body condition, consistent with the conclusions of Soeffker et al. (2022). This may reflect the flexibility in diet of Patagonian toothfish, which is both a scavenger and active predator, able to switch readily to whatever is the most abundant resource (Collins et al., 2007, 2010; Roberts et al., 2011). The fluctuations in condition in the different maturity stages are consistent with expectations, as stage four represents their spawning peak, when gonads are fully developed and represent a considerable proportion of overall body weight (Everson and Murray, 1999).

4.3. Catch per unit of effort

CPUE declined from the early years of the fishery to 2010–2012, which is probably related to a decrease in toothfish abundance, including from IUU fishing (Agnew and Kirkwood, 2005). Such a decrease is consistent with CCAMLR decision rules (Constable et al., 2000) and the current stock assessment (CCAMLR, 2023), which indicates that the stock is currently just below 50 % of the pre-exploitation biomass. This trend is expected in fisheries and has been recorded for Patagonian toothfish in other areas (Lord et al., 2006; Duhamel et al., 2011) and species such as Atlantic cod in the northwest Atlantic Ocean (Nogueira et al., 2015), pollock (*Pollachius pollachius*) in northeast Atlantic Ocean (Casini et al., 2005), orange roughy (*Hoplostethus atlanticus*) and black cardinalfish (*Epigonus telescopus*) in New Zealand (Hilborn et al., 2006; Dunn, 2009). In all cases the highest CPUE was found at the start of exploitation. This can be countered or managed by improvement in fishing methods, fleet efficiency, and knowledge of the fishing grounds (Maunder and Watters, 2001). Management at South Georgia also had a key influence on CPUE, through the depth restrictions imposed (Table 1), affecting the availability of fish of different sizes, ages and sex, and the spatial distribution of fishing, through the establishment of Benthic Closed Areas. Nonetheless, factors external to fishing operations such as environmental conditions and depredation (Söffker et al., 2015) may also influence CPUE (Trathan et al., 2014; Brooks et al., 2018). Hence, regulatory changes after 2012 led to standardisation of fishing operations (including quotas, depths, number of vessels), and the CPUE is now broadly stable.

4.4. Conclusions

Ultimately the trends observed here in terms of population structure of Patagonian toothfish, are not ecologically significant, with no evidence of overexploitation. The trends in population structure are likely the result of natural fluctuations in length as a function of recruitment variability, and the biggest change seen in the late 1990s was mainly due to the lack of regulation in previous decades. Fisheries management around South Georgia has been evaluated and improved continuously, and the ecosystem-based approach advocated by CCAMLR has been effective, evidenced in the size at maturity results presented here. Based on our results, a further refinement in terms of regulations could be to increase the depth limit in years or periods when trawl surveys (e.g., Collins et al., 2007) indicate strong recruitment (identified by routine surveys), thus safeguarding future recruitment to the fished population, which would be beneficial both for the fishery and the ecosystem.

CRedit authorship contribution statement

Richard Phillips: Conceptualization, Methodology, Supervision, Writing – review & editing. **Connor Bamford:** Methodology, Writing – review & editing. **Martin Collins:** Conceptualization, Data curation, Formal analysis, Methodology, Supervision, Writing – review & editing. **José Abreu:** Conceptualization, Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **José Xavier:** Conceptualization, Supervision, Writing – review & editing. **Philip Hollyman:** Conceptualization, Data curation, Formal analysis, Methodology, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.fishres.2024.107122](https://doi.org/10.1016/j.fishres.2024.107122).

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