Spatial, temporal, and demographic variability in patagonian toothfish (*Dissostichus eleginoides*) spawning from twenty-five years of fishery data at South Georgia

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ABSTRACT

Patagonian toothfish (*Dissostichus eleginoides*) are a commercially important species that support a longline fishery at the subantarctic island of South Georgia (CCAMLR Subarea 48.3). Understanding the life history of Patagonian toothfish is key to the successful management and sustainability of this fishery. Using catch data from the past 25-years, 1997 to 2021, we provide an updated assessment of the spatial, temporal, and demographic variability of Patagonian toothfish spawning at South Georgia. Our findings confirm that spawning occurs in the vicinity of the shelf-break of South Georgia, with significant spawning hotspots detected at Shag Rocks, midway along both the northern and southern shelf breaks, and at the eastern end of the island. The location of these hotspots were consistent over the 25-years examined. Based on data between 1997 and 2007, when fishing occurred routinely all around the island and at Shag Rocks, 40% of detected hotspot locations overlapped with regions where Benthic Closed Areas (BCAs) were established in 2008. With this, we can estimate that approximately 40% of spawning hotspots are located within, and already protected by, the existing network of BCAs. There was evidence that the timing of toothfish spawning exhibited bimodality at South Georgia with a peak in April being observed in the first two years of the time series. This peak fell outside the seasonally restricted fishing season for many subsequent years. These findings are discussed in the context of both historic, current, and possible future regulatory changes to this longline fishery.

1. Introduction

A species' reproductive traits, including their timing and location of spawning are well established as being key to the life-cycle of populations (Hjort, 1914, 1926). These strategies form over millennia and are influenced by a balance between the species' biology and features of their environment. Reproductive characteristics, such as age at maturity, size at maturity, timing and duration of spawning, are often dynamic, and are influenced by environmental factors (e.g. temperature, Pankhurst and Munday, 2011). As a result, these population level patterns can shift in response to environmental changes (Morgan, 2008; Rideout and Tomkiewicz, 2011; Scott and Pankhurst, 1992). However, spawning patterns can also shift because of significant harvesting pressure, inducing changes in a species' demographic and reproductive traits

(Huthchings and Fraser, 2008; Ohlberger et al., 2022). As such, there is a need to consider both demographic strategies (Ohlberger et al., 2022), as well as spatiotemporal measures into management considerations, which act to safeguard key life stages of fish populations.

In the Southern Hemisphere, there are two species of endemic toothfish: the Antarctic toothfish (*Dissostichus mawsoni*), and the Patagonian toothfish (*D. eleginoides*). Both share circumpolar distributions, with *D. eleginoides* found at lower latitudes than *D. mawsoni*, notably around the sub-Antarctic islands and the coast of South America (Collins et al., 2010; Hanchet et al., 2015). The distribution of these two species is known to overlap in the mid-to-high latitudes, for instance, such an overlap occurs at the South Sandwich Islands (Soeffker et al., 2022). However, it is believed that *D. eleginoides* is limited from accessing higher latitudes due to the lower water temperatures close to the

Antarctic continent and an inability to produce antifreeze glycopeptides (Collins et al., 2010; Eastman et al., 1990). In the South Atlantic, populations appear to be distinct, with those at South Georgia differing genetically from those on the Patagonian shelf or other regions of the Southern Ocean (Rogers et al., 2006; Shaw et al., 2004). Arkhipkin et al. (2022) recently proposed that Patagonian toothfish north and south of the Polar Front represent distinct species and that *D. eleginoides* south of the Polar Front be considered *D. australis*. Here, we use the current nomenclature *D. eleginoides* for the South Georgia fish, with these being referred to as Patagonian toothfish or toothfish hereafter.

Patagonian toothfish are a long-lived (>50 years) scavenging species, which grow rapidly in relatively shallow waters, before migrating ontogenetically into deeper waters as they grow. This species generally adheres to a bigger: deeper pattern (Coggan et al., 1996; Collins et al., 2007; Laptikhovsky et al., 2006; Lord and Duhamel, 2006). At South Georgia, juvenile toothfish predominate at depths of 100–300 m, whilst maturing and adult fish are more commonly found at depths between 700 and 2000 m (Collins et al., 2007). However, adult toothfish have been observed to occur on the continental shelf in the Falkland Islands (Laptikhovsky et al., 2006), and have been caught, albeit in low abundance, on the South Georgia shelf (Collins et al., 2007) and in deep (~200 m) coastal fjords (Collins, pers. comm.). Typically, male toothfish reach sexual maturity at between 6 and 10 years and at 69.6 ± 9.3 cm (Total length, TL ± Standard Deviation, SD), whilst females mature later, at between 10 and 13 years and 98.9 ± σ10.1 cm (TL ± SD) (Agnew et al., 1999; CCAMLR, 1987; Everson and Murray, 1999; Moreno, 1998).

Toothfish recruitment at South Georgia is episodic in nature (Belchier and Collins, 2008; Collins et al., 2007, 2010) and has been inversely correlated with sea surface temperature (Belchier and Collins, 2008). On the Patagonian shelf, intervals between recruitment pulses have been shown to be approximately four years (Laptikhovsky and Brickle, 2005) but are less well understood at South Georgia. Fluctuations in recruitment appear to be more irregular and have been observed as strong pulses in trawl survey catch data. These have been recorded in 2003 (Collins et al., 2007) and again in 2011, 2021 and 2023 (BAS, unpublished data). Geographically, the shelf edge of South Georgia is strongly associated with toothfish spawning (Agnew et al., 1999; Brigden et al., 2017) and hotspots have previously been identified at both the eastern and western ends of the island, in waters *ca.*1200 m deep (Brigden et al., 2017; Söeffker et al., 2014b). This differs from spatial patterns observed on the Patagonian shelf, where spawning occurs south of the Falkland Islands in an easily delineated region, on the Burdwood Bank in waters *ca.* 1000 m (Laptikhovsky et al., 2006; Laptikhovsky and Brickle, 2005). The shelf surrounding Shag Rocks, located to the east of mainland South Georgia (Fig. 1), appears to be an important nursery ground for juvenile toothfish (Belchier and Collins, 2008). At this location, reduced predation risk (Reid et al., 2007) and access to prey (Collins et al., 2007) may favour juvenile survivability.

At South Georgia, toothfish have been shown to display a dual-peak in spawning, with a smaller event occurring in April/May followed by a significantly larger peak in July/August (Agnew et al., 1999). The timing of this larger peak differs slightly, although not substantially, from the April/May peak observed at Kerguelen (Lord and Duhamel, 2006), and the June/July peak on the Chilean coast (Arana, 2009). Brigden et al. (2017) suggested that since 1997, at South Georgia, female spawning has shifted later in the year, effectively shortening the spawning season. The timing of spawning events, and their need to coincide with favourable bio-geophysical conditions has been linked with reproductive success (Wright and Trippel, 2009). Thus, there is a need to improve our understanding of spawning dynamics, particularly in light of the active fishery for this species in the Southern Ocean.
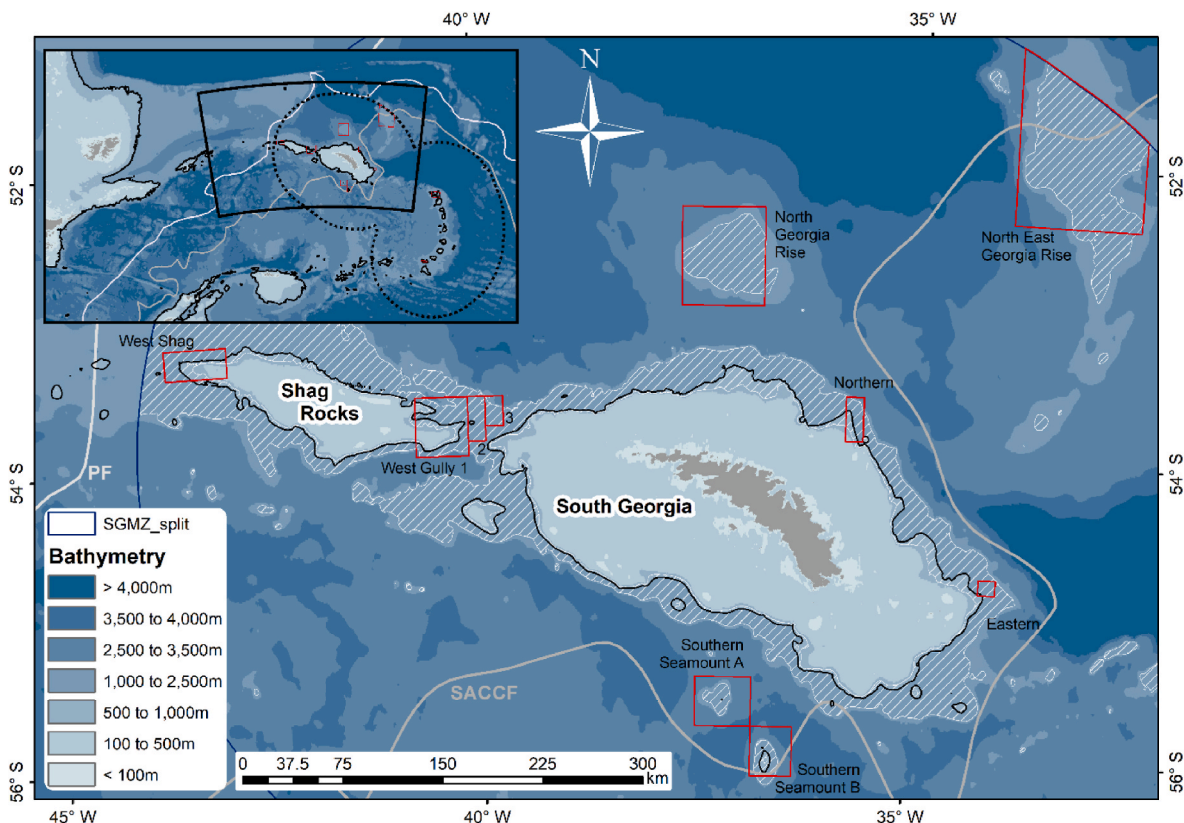
Fig. 1. Study area showing the position of the Benthic Closed Areas (BCAs, red boxes) around South Georgia. The black line denotes the 1000 m bathymetric contour; the black box in the contextual panel shows the limits of CCAMLR Subarea 48.3. The light grey line labelled PF denotes the mean position of the Polar Front, and the darker grey line labelled SACCF denotes the mean position of the Southern Antarctic Circumpolar Current Front (Orsi et al., 1995; Trathan et al., 2000). The white hashed areas indicate the 700 m–2250 m bathymetric range within which the toothfish fishery is currently permitted to operate.

The quality of toothfish meat made this species an alluring target and subsequently the focus of highly lucrative, large-scale fisheries. At South Georgia, a longline fishery began in the late 1980s (Collins et al., 2010) and peaked, in terms of catch, in 2003 with 7485 tonnes caught. Since this peak, catch limits have been restricted by CCAMLR (and domestic regulations), and since 2011 catches have been relatively stable (Collins et al., 2021) ranging between 1732 and 2196 tonnes annually (Fig. 2). Pre-2006, the fishery typically implemented the 'Spanish' longline system, whereby hooks are attached to fishing line that is connected to the main line by a series of vertical weighted lines, whereas post-2006 the fleet transitioned towards using the 'autoline' gear system (Collins et al., 2010). The main difference between the two systems is that Spanish gear allows the hooks to drift slightly higher above the sea floor than is possible when using the 'autoline' system (Benedet, 2017) and the 'autoline' system uses smaller pieces of bait.

In its early years, between 1988 and 1993, the toothfish fishery operated year-round. However, due to concerns raised over seabird by-catch the season was subsequently restricted to the winter months (Collins et al., 2021). At the time, this restriction to the fishing season was noted to cause overlaps with the spawning season of Patagonian toothfish (CCAMLR, 1999), which spawn at South Georgia during the austral winter (Agnew et al., 1999; Evseenko et al., 1995; Kock and Kellermann, 1991); a pattern reflected similarly elsewhere in the Southern Hemisphere (Arana, 2009; Laptikhovsky et al., 2006; Lord and Duhamel, 2006). The operational period for the longline fishery at South Georgia has seen a complex set of alterations to its start and end dates over the past two decades (Collins et al., 2021), along with specific regulations on permitted gear and depth ranges. These alterations to the operational remit of the fishery balance spatial and temporal overlaps and act to safeguard both conservation objectives and the economics of the fishery, which is known to observe a drop in catch during the spawning season (Clark and Agnew, 2009).

The South Georgia toothfish fishery has been certified as sustainable by the MSC since 2004 (Marine Stewardship Council, 2022). To inform and update the management of the South Georgia toothfish fishery an up-to-date understanding of the demographics and distribution of Patagonian toothfish at South Georgia are required. Building on the work of Brigden et al. (2017), in this paper we utilise an additional 7 years of data and present a collection of analyses that explore the spatial, temporal, and demographic patterns of Patagonian toothfish spawning

at South Georgia. Here we consider a 25-year period from 1997 through to 2021, inclusively, during which good quality observer data is available. We then contextualise these analyses and discuss them in relation to the current understanding of the seasonality and drivers of toothfish reproduction alongside the management measures, notably the spatial closures associated with the BCAs.

2. Methods

The sub-Antarctic archipelago of South Georgia and the South Sandwich Islands is located in the Southern Ocean, approximately 1000 km south-east of the Falkland Islands, inside the Commission for the Conservation of Antarctic Marine Living Resources' (CCAMLR) Subarea 48.3 (Fig. 1). Mainland South Georgia lies within the dynamic easterly flow of the Antarctic Circumpolar Current, to the south of the Polar Front, which isolates the region from South America, and to the north of the Southern Antarctic Circumpolar Current Front (Orsi et al., 1995; Trathan et al., 2000). The shelf of South Georgia is bathymetrically (Hogg et al., 2017) and oceanographically complex (Young et al., 2014), with deep gullies acting as channels for both on and off-shelf currents (Young et al., 2014). The shelf itself extends >100 km offshore at points, where it breaks abruptly, and depths rapidly exceed 3000 m. Approximately 240 km to the west of mainland South Georgia lie Shag Rocks, a group of six small outcrops that are separated from the main continental shelf by a deep gully that exceeds several km deep. The South Georgia shelf is characterised by higher than average productivity, which reaches levels that far surpass the background productivity of the wider Southern Ocean (Atkinson et al., 2001; Korb and Whitehouse, 2004).

2.1. Data used

Under CCAMLR Conservation Measures, fishing vessels are required to report details of their catch, including location, depth, number of hooks deployed and any by-catch, on a haul-by-haul basis (CCAMLR C2). Scientific observers are required to be present on all fishing vessels within the CCAMLR Convention Area. These observers are tasked with collecting standardised biological data on target species along with data on bycatch within the fishery. Data are available on request from the CCAMLR Secretariat. Here we requested catch and effort data (CCAMLR C2) and biological data (Observer Data) from the South Georgia
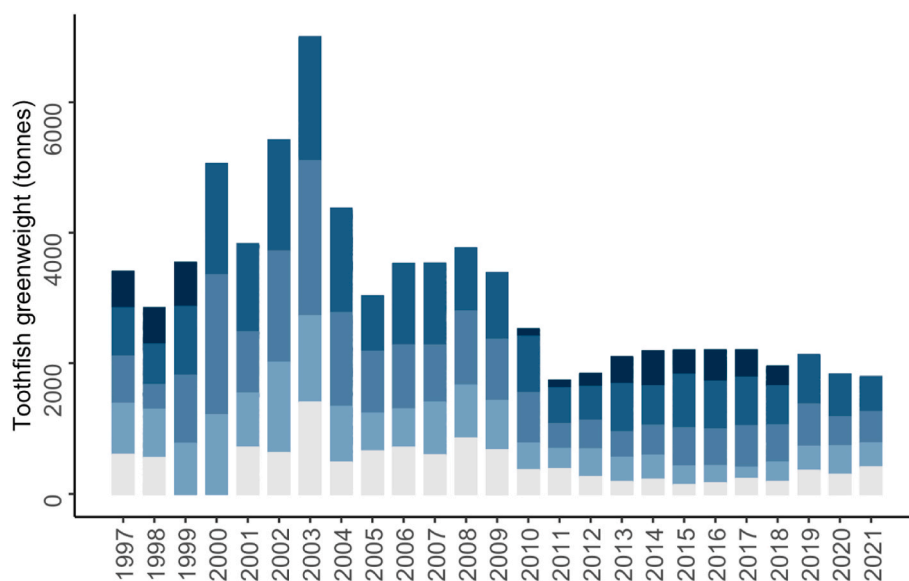

Fig. 2. Patagonian toothfish catches between 1997 and 2021 for the toothfish fishery operating at South Georgia within the Conservation of Antarctic Marine Living Resources' (CCAMLR) management Subarea 48.3. Each year is colour coded to show the monthly contributions to total annual catch; from dark to light: ■ April; ■ May; ■; June; ■ July; ■ August (CCAMLR, 2022).

toothfish fishery in Subarea 48.3. These requested data spanned the period from 1985 to 2021. However, data were inconsistently sampled in the early years of this fishery and, as a result, we are only considering data from 1997 onwards. Due to variations over time in the seasonal closure of the fishery, monthly data are also unevenly represented. As such, we considered data from April to August, inclusively. Most of the Patagonian toothfish catches in Subarea 48.3 are caught near the shelf-break or over the shelf of South Georgia. However, 0.81% (n = 3147) of the catch records were spatially anomalous and were caught away from this main region either to the west of Shag Rocks or further north. To investigate spawning dynamics near South Georgia, data were truncated to remove records to the west of 45°W and to the north of 51°S.

Several metrics underpin our analyses, these are: (i) sex and maturity stage of the sampled fish (Observer Data); (ii) number of hooks per line (C2); (iii) green weight of toothfish caught per line (C2); and (iv) location and depth that the line was set (C2). These were extracted from the combined catch, effort and biological datasets and totalled 382,524 records. Depth data were missing from 0.1% (n = 429) of the data, and these values were repopulated from General Bathymetric Chart of the Oceans bathymetric data (GEBCO Bathymetric Compilation Group, 2020). Further records with missing data were removed with this representing 5.1% of this initial dataset (n = 32,211). For the remaining records, sea surface temperature were extracted using the R package *'rerddapXtracto'* v1.0 (Mendelssohn, 2020), which accesses the National Oceanic and Atmospheric (NOAA) Southwest Fisheries Science Centre (SWFSC) data servers to extract data from the *'NOAA_DHW_monthly'* dataset due to its matching temporal and spatial extents at a spatial resolution of 5 km^2.

Biological records detailing information on fish maturity stage followed the classification of Kock and Kellermann (1991), see Table 1, with sampling of the catch adhering to the protocols set out in the CCAMLR Scientific Observer's manual (CCAMLR, 2020). To provide a measure of abundance, CPUE was calculated for each set line as kilograms (kg) of caught toothfish 1000 hooks^{-1}. Data from autoline and Spanish fishing systems were pooled for our analyses. Where appropriate we distinguished between fishery level CPUE and CPUE of stage 4 spawning fish by referring to the latter as catch rates of stage 4 spawning fish or by using *spawning* CPUE (sCPUE). As maturity data were only available from the CCAMLR observer subsample, there was a need to extrapolate the observed rates of maturity stages to the remaining catch data; this produced prorated CPUE values. To do this the total sampled weight on each set line was calculated for each maturity stage and sex combination. Data were then grouped by line, sex and maturity stage. For each of these summarised records averages were calculated for the number of hooks per line (α); green weight of toothfish caught on each line (β); green weight of the sampled toothfish (γ); and the sum of green weight for each maturity stage (δ). These were then used to estimate a proportional CPUE (Ω), following : $\varepsilon = \delta/\gamma$; $\theta = \beta \times \varepsilon$; $\Omega = (\theta/\alpha) \times 1000$, where ε and θ represent an intermediary quotient and product, respectively. These calculations provided a proportional estimate of

CPUE that was individual to each longline set and accounted for the different proportions of maturity stages and sex within the catch data. Our analyses were based on this adjusted data. Lines were infrequently hauled without any toothfish being caught; this occurred in 8.4% (n = 30,485) of lines set. These lines were removed from the analysed data. Our final dataset was comprised of 109,624 records, of which 14.3% (n = 15,719) were classified as stage 4 spawning fish over a 25-year period. Annual samples (lines) ranged from 2060 in 1997 to 9096 in 2003 over all maturity stages, and between 224 in 2015 and 1316 in 2009 for stage 4 fish. Here we use the terms 'spawning', 'gravid' (female) or 'ripe' (male) interchangeably when referring to stage 4 classified toothfish.

Since 1995, the Patagonian toothfish fishery has been restricted to winter, due to the high risk of seabird by-catch at other times of the year. Whilst the season start date has varied slightly, and there was some experimental fishing in February 1999, detailed observer data is available for the fished period each year, with monthly coverage varying between April and August over the period 1997 to 2021; we present results over these years.

2.2. Spatial patterns of toothfish spawning

To identify spawning hotspots around South Georgia the Getis-Ord Gi* statistic was implemented in the R package *spdep* (Bivand et al., 2013; Bivand and Wong, 2018). This metric, also referred to as a hotspot analysis (HSA), examines spatial autocorrelation in aggregated data, taking into account both a spatial component (latitude and longitude) and a weighting factor, here catch rates of spawning fish, to identify locations where the value of the weighting factor is above what would be expected due to random chance (Getis and Ord, 1992; Ord and Getis, 2001). The Getis-Ord Gi* statistic is given by:

$$G_i^* = \frac{\sum_{j=i}^{n} \omega_{i,j}\chi_j - \overline{X} \sum_{j=i}^{n} \omega_{i,j}}{s\sqrt{\left[n\sum_{j=1}^{n} \omega_{i,j}^2 - \left(\sum_{j=i}^{n} \omega_{i,j}\right)^2\right]}}$$

When x_j is the attribute value for the feature, $\omega_{i,j}$ is the spatial weight between feature i and j, n is equal to the total number of features and:

$$\overline{X} = \frac{\sum_{j=1}^{n} x_j}{n} \quad s = \sqrt{\frac{\sum_{j=1}^{n} x_j^2}{n} - (\overline{X})^2}$$

With the G_i^* statistic reporting the spatial associations as Z-scores, with each location being examined in the context of its neighbours (in this case the nearest 10), no further calculations are required. To interpret these Z-scores, features that display spatial clustering are assigned high positive Z-scores (hotspots), and those that display a lack of spatial clustering are assigned low negative Z-score (coldspots). The significance of these outputs were calculated and determined by P-

Table 1

Maturity scale for male (♂) and female (♀) Patagonian toothfish (*D. eleginoides*) applied in the South Georgia fishery, after Kock and Kellermann (1991).

♂				♀
Description	Maturity	Stage	Maturity	Description
Testis small, translucent, whitish, or long with thin strips lying close to vertebral column	Immature	1	Immature	Ovary small, firm, no eggs visible to the naked eye
Testis white, flat, convoluted, easily visible to the naked eye, about a quarter of the length of the body cavity	Developing or resting	2	Maturing virgin or resting	Ovary extended, firm, small oocytes visible, giving the ovary a grainy appearance
Testis large, white, and convoluted, no milt produced when pressed or cut	Developed	3	Developing	Ovary large, starting to swell in the body cavity, colour varies by species, contains oocytes of two sizes
Testis large, opalescent white, drops of milt produced when pressed or cut	Ripe	4	Gravid	Ovary large, filling or swelling in the body cavity, when opened large ova spill out
Testis shrunk, flabby, dirty white in colour	Spent	5	Spent	Ovary shrunken, flaccid, contains few residual eggs and many small ova

values after applying a Bonferroni adjustment to reduce the incident rate of false positives within the data (Bivand et al., 2013; Bivand and Wong, 2018). Pooling data from all years, we carried out HSA for spawning toothfish (stage 4, gravid/ripe) for each available month (April to August, inclusively). We also conducted an HSA on five 5-year tranches of the data to examine temporal trends in the spatial distribution of spawning activity around South Georgia; the periods examined were (i) 1997–2001; (ii) 2002 to 2006; (iii) 2007 to 2011; (iv) 2012 to 2016; and (v) 2017 to 2021. A measure of overlap between the detected hotspots over the entire timeseries and the BCAs was calculated by applying a 8.3 km diameter buffer to all locations >95% significance using projection EPSG:3762; this buffer corresponds to the median distance of annual toothfish movement (Soeffker et al., 2022).

2.3. Temporal changes in catch rates of spawning fish

Diagnostic plots along with generalised linear models (GLMs) were used to investigate the variation in catch rates of spawning fish over the duration of the time series. GLMs with a negative binomial structure and a log link function were fitted to both male and female stage 4 spawning fish data in the R package *MASS* (Venables and Ripley, 2002). The response variable was sCPUE and the explanatory covariates were year, depth, Julian day, region (Shag Rocks or South Georgia) and sea surface temperature (after Belchier and Collins, 2008). Candidate covariates were checked for collinearity using pair plot matrixes. Collinearity was detected between sea surface temperature and Julian day for both sexes ($\male$: 0.69; $\female$: 0.77). Consequently, Julian day was removed as a covariate.
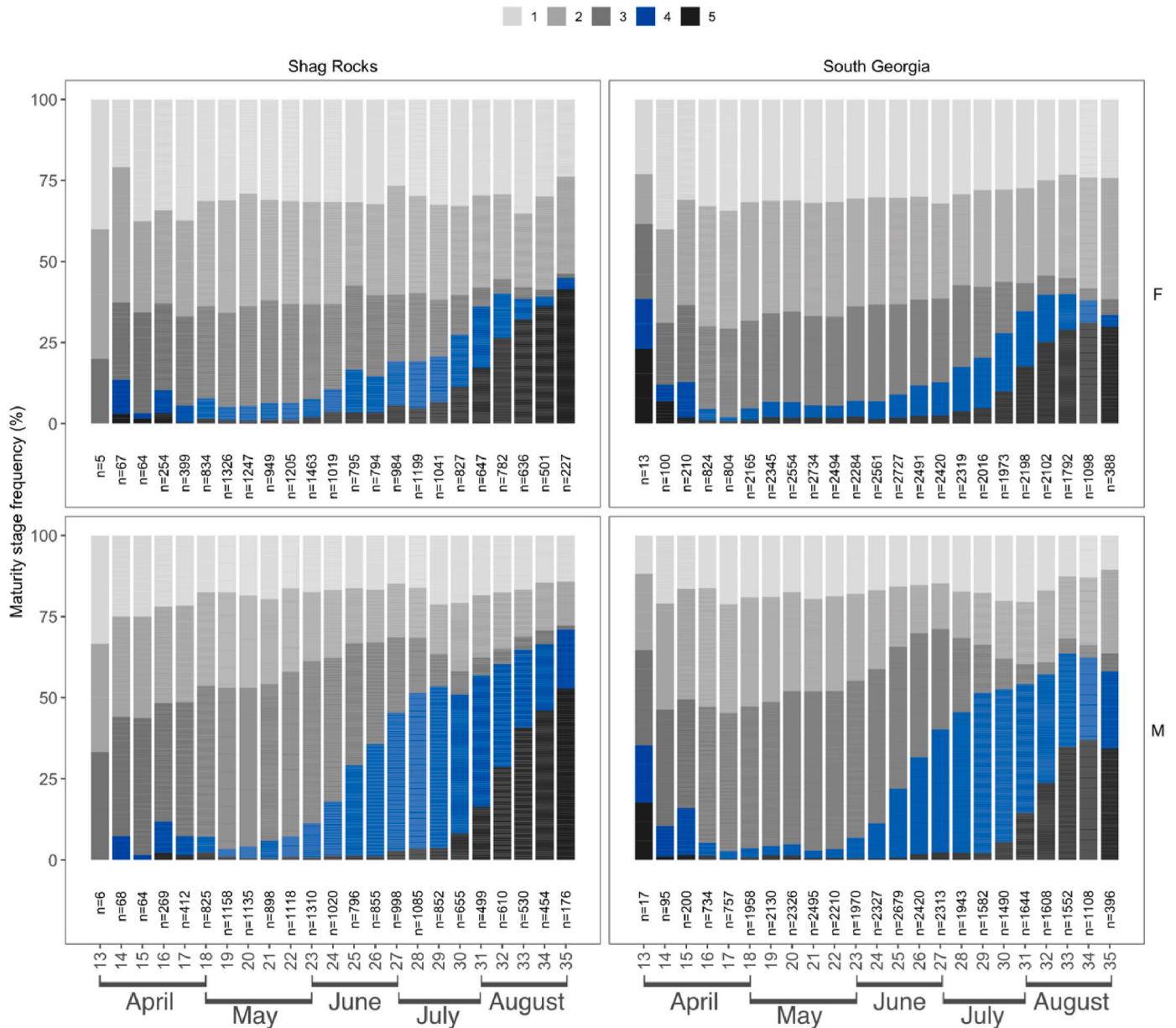

Fig. 3. Proportion of maturity stages caught throughout the licensed fishery season (April to August), here denoted in weeks of the year between April and August, inclusively. An incremental colour scale is used to identify the maturity stages, after Kock and Kellermann (1991). Stage 1 fish are denoted by ▢; stage 2 by ▨; stage 3 by ▨; stage 4 by ▧; stage 5 by ■. The left column represents fish caught to the west of 40°W (i.e., Shag Rocks), and the right column those fish caught to the east of 40°W (i.e., South Georgia), with the top row representing data from female fish, and the bottom from male fish. Sample sizes for each subdivision of the data are indicated below their respective column.

3. Results

3.1. Temporal patterns in spawning

Data from observers showed clear patterns in the proportion by maturity stage for both sex and location of the toothfish catch (Fig. 3). In both geographic locations, maturity stages 1–3 dominated the catch in the early weeks of the season with the proportion of stage 4 (spawning) fish in the catch greatly increased for both sexes and both locations at approximately the 22nd week (late May). After the peak in spawning, at approximately the 30th week (late-July), stage 5 (spent) fish were observed in the catch at much higher levels than earlier in the season. Sex differences also appeared in the data as the season progressed, with stage 4 spawning males representing a much higher proportion of the catch from the 25th week (mid-June) onwards at both Shag Rocks and South Georgia. There was also evidence of an earlier spawning peak in early April, but there was limited data from this time (only 1997 and 1998).

Trends in the catch rates of spawning fish over the whole time series (1997–2021) were examined for each sex using generalised linear models (Table 2) to highlight factors that influenced spawning. For both sexes, these models affirm the small decrease in catch rate of spawning fish between 1997 and 2021, previously reported in Earl and Readdy (2022). For females, depth showed a significant positive correlation with sCPUE, with deeper waters associated with slightly higher sCPUE, whereas for males there was a slight negative correlation. Regionally, there was a significant difference between catches at Shag Rocks versus South Georgia, with the latter being associated with lower spawning catch rates in both sexes. Finally, over this time series there was variation in the impact of sea surface temperature between the sexes, with warmer waters being associated with higher sCPUE in females, with an inverse pattern, although non-significant, observed in males. Within the season, CPUE, by weight, was higher earlier in the season (Fig. 4).

The proportion of spawning fish in the catch was not consistent through the season (Fig. 4a). Over the 1997 to 2021 time series, there was an increase in the spawning component of the catch from week 23 onwards, with the number of stage 4 spawning fish caught peaking in July. This peak in the proportion of spawning fish in the catch corresponded to a decrease in fishery CPUE in late June and July (Fig. 4b). Additionally, there was evidence of an earlier peak in spawning activity as there was an initial decrease in spawning fish caught in weeks 13–16. However, the fishery season has never operated early enough to detect this possible peak in its entirety.

Although the linear models identify a statistically significant shift towards later spawning, the scale of the change was minimal, and both metrics vary depending on the component of the data examined (Table 3). Over the whole time series, 1997 to 2021, the mean date of spawning shifted by 0.026 days per year ($R^2 = 0.011$, Fig. 5 black line). However, due to the bimodality in the spawning catch where there is evidence of an earlier peak in spawning activity (see Fig. 4a), if the same

model is fitted to the years of the time series when the fishery opened later (1999 onwards), and this earlier peak is excluded, mean spawning date has shifted by 0.008 days per year ($R^2 = 0.001$, Fig. 5 red line) (Table 3).

Spawning fish were caught at an average depth of 1208 m (SD: ±348 m) over the 25-year time series and over this time the depth at which spawning fish were caught increased (Fig. 6a). Within the season, the depth at which spawning fish were caught varied between locations for both sexes (Fig. 6b). At Shag Rocks sample sizes were smaller and the data showed greater variability, with females displayed a deepening trend at the start of the season though until approximately the 24/25th week at which a shallowing occurred over the next five weeks. This was then followed by a gradual shift towards deeper waters at the end of the season. Patterns for males at Shag Rocks show that initially, spawning fish were caught in slightly deeper waters. However, as the season progressed the depth at which they were caught shallowed to a peak that lagged the female peak by a few weeks. This shallowing trend then reverted into a shift towards deeper waters for the rest of the season. Conversely, at South Georgia spawning depth remained broadly constant throughout the season with a slight shallowing occurring for both sexes, although this is more noticeable for male fish, at about the 26–28th week mark.

3.2. Spatial patterns in spawning

Over the 25-year time series at South Georgia the effort of the toothfish fishery focussed on the shelf break of the archipelago, and whilst catches were taken around the entire island, there was evidence that there were regions of more intense fishery activity (number of hooks) (Fig. 7). There were three regions of higher activity; (i) to the west of the Northern BCA; (ii) on the southern shelf break of the island, due north of the Southern Seamount BCAs; and (iii) towards the western end of the Shag Rocks' shelf break.

Spawning hotspots were investigated for each month between April and August, inclusively, and for five 5-year periods from 1997 to 2021. These analyses were based on pooled male and female catch data. The HSA identifies spatially significant clustering of sCPUE values within the catch data compared to an assumed random background spatial process (Table 4). At each location (i.e., latitude/longitude defined catch data-point) results come in the form of a Z-value, of which the associated significance has been classified for both hot- and cold-spots as either >99% significance or > 95% significance. Hotspots are depicted in red, and coldspots in blue with the darker of each respective colour indicating the higher significance threshold. Non-significant values are depicted in grey.

Over the length of the 25-year period the HSA indicated that the spawning of Patagonian toothfish was associated with the shelf break around both South Georgia and Shag Rocks (Fig. 8), and along this bathymetric contour there were clear areas where spawning was more clustered. An examination of the overlap between the detected hotspots

Table 2
Results of the generalised linear models for spawning (stage 4) Patagonian toothfish between 1997 and 2021. Catch per unit effort of spawning fish (sCPUE: kg per 1000^{-1} hooks) was the response variable. Female sample of 4784; male sample of 10,050.

	Coefficient	Estimate	Standard Error	Z value	P value	Deviance			
						Residual	df	Null	df
Females	Intercept	50.1250	3.6721	13.6502	P < 0.0001	5390.4	4779	5691	4783
	Year	−0.0229	0.0018	−12.5161	P < 0.0001				
	Depth	0.0002	0.0000	3.9449	P < 0.0001				
	Region South Georgia	−0.2173	0.0317	−6.8581	P < 0.0001				
	Sea surface temperature	0.0971	0.0198	4.9095	P < 0.0001				
Males	Intercept	54.8153	3.0528	17.9555	P < 0.0001	11,359	10,045	12,139	10,049
	Year	−0.0250	0.0015	−16.3831	P < 0.0001				
	Depth	−0.0003	0.0000	−10.8623	P < 0.0001				
	Region South Georgia	−0.1998	0.0230	−8.6941	P < 0.0001				
	Sea surface temperature	−0.0030	0.0166	−0.1789	0.858				
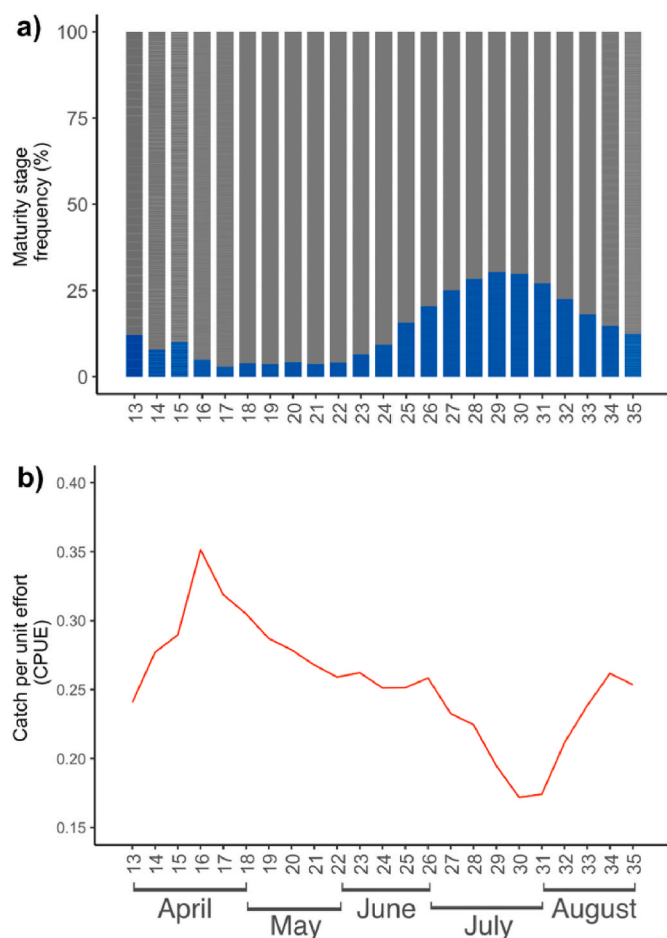
Fig. 4. a) The proportion of the sampled catch that were classified as stage 4 spawning (blue) versus stages 1–3 and 5 (grey) for each week of the season between 1997 and 2021. b) Total Catch Per Unit Effort (CPUE, kg per 1000^{-1} hooks) of the fishery over all maturity stages for each week of the season between 1997 and 2021.

(>95% significance) and the BCA boundaries (Table 5) show that prior to the establishment of the BCAs (1997–2007), when fishing was less spatially restricted, 39.7% (n = 564) of the total detected hotspots (n = 1421) occurred within the regions where BCAs were later established. The spatial biasing of the data, triggered by the prohibition of fishing within the BCAs, is then linked to a lower overlap of just 6.1% (n = 79) when data from after the BCA establishment is considered.

Beginning at the north-west tip of the island chain there was evidence for a clear spawning hotspot that overlaps with the West Shag Rocks BCA, and then isolated instances of spawning activity along the northern shelf-break of Shag Rocks before spawning peaks again, overlapping with the West Gully BCA. Whilst spawning occurs all along the South Georgia shelf-break, hotspots were prevalent to the west and south-east of the Northern BCA, and then to the south of the Eastern BCA. Isolated hotspots were present along the southern shelf-break of South Georgia, due north of the Southern Seamount BCAs, and then isolated clusters were present along the remaining southern shelf-break of South Georgia and extending along the same contour line to the south of Shag Rocks.

Patterns were broadly consistent between female and male toothfish (Fig. 9), with spawning occurring around the entirety of the shelf break of Shag Rocks and South Georgia. Of note, was an apparent variation in spawning dynamics between the sexes that occurs on the southern shelf break of Shag Rocks where females appeared to display more spawning hotspots compared to males, which, whilst present in this region appeared not to aggregate in as many significant clusters. Males also displayed greater prevalence of coldspots around the entirety of this regions shelf break.

Locations of hotspots were largely consistent through the season (Fig. 10). However, the intensity of the identified clustering varied because of the sample size difference between April and the peak in July. Of note here was the non-significant Getis-Ord Gi* statistic for April, meaning that patterns detected in this month may have been due to chance and not part of an underlying spatial process in the aggregation of the catch data. Here we included this result for context. From May onwards, spawning appeared to increase, and more hotspots were detected as the season progressed. There also appeared to be a longitudinal progression from west to east through the season, with more spawning in the west earlier in the season. However, this was potentially linked to a spatial bias in fishing effort.

The hotspot analyses in five-year tranches from 1997 through to 2021 (Fig. 11), provides evidence that spawning exhibits localised shifts over the time series examined, along with regions playing host to spawning hotspots in some periods and not others. Here, it is important to note that in 2008 the West Shag, West Gully BCAs and the Northern BCAs were all closed and hence these did not appear as hotspots in subsequent years. For instance, the northern shelf break of South Georgia to the west of the Northern BCA (~34°W to 36°W) displayed an aggregation of hotspot signatures in all examined periods other than between 1997 and 2001, and between 2007 and 2011. Additionally, at the south-eastern tip of the South Georgia shelf, a small, localised hotspot was present between 1997 and 2001 and in 2007–2011, but absent in other years, suggesting a potential cyclical reoccurrence of spawning in these locations. However, there are also several persistent spawning hotspots that were present, in varying degrees, throughout the time series. The hotspot that occurred directly to the west of the Northern BCA (~36°W - 37°W), whilst not present between 1997 and 2001, was present in all other examined periods. Of additional note are the hotspots that occurred in the vicinity of both the Western Shag BCA and the West Gully BCA, which were persistent throughout the 25-year period.

4. Discussion

Here we provide an updated assessment of the spatial, temporal, and inter-annual variability in Patagonian toothfish spawning at South Georgia using a 25-year time series from 1997 to 2021. In interpreting this time series, it is important to consider the changes in the regulation and operation of the fishery over time, many of which were introduced to reduce the impact of the fishery on non-target species (Collins et al., 2021; Trathan et al., 2014). The ecological role of these relatively long-lived predatory fish, alongside the economic significance of this fishery to the region means that the sustainable management of this resource is of the upmost importance. Patagonian toothfish recruitment at South Georgia is episodic in nature (Belchier and Collins, 2008; Collins et al., 2007, 2010), and understanding where and when this occurs is important to both our understanding of this species and to ongoing management. This study provides such an assessment and builds on existing knowledge, presenting new findings relating to the

Table 3
Results of a linear model relating year to the Julian day of spawning activity throughout two portions of the time series.

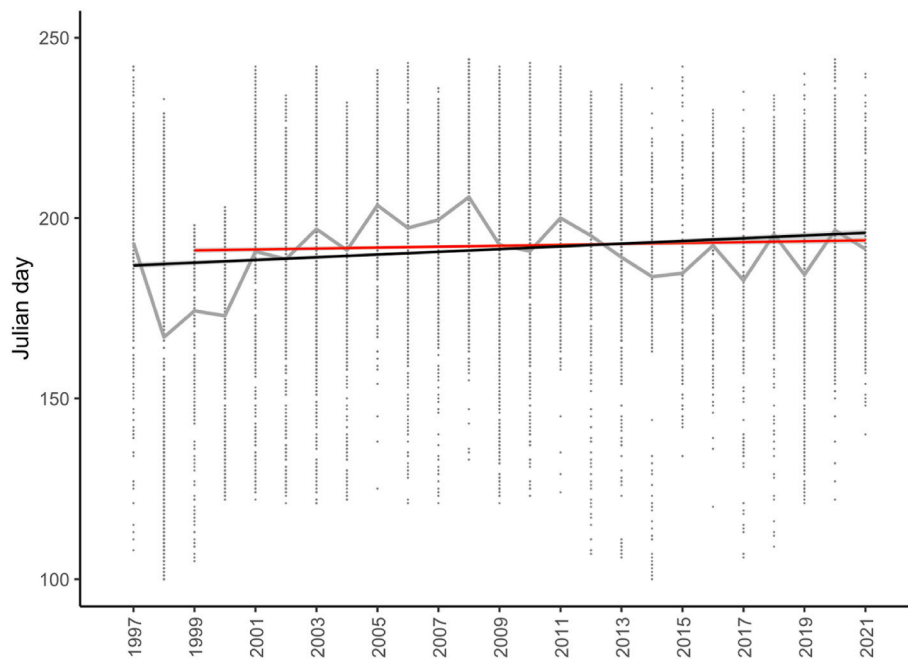| Model	Coefficient	Estimates	SE	T value	P value	Residual SE	df	F stat	R^2
1997 to 2021	Julian Day	0.026	0.002	3.14	P < 0.001	6.8	15,717	172.7	0.011
1999 to 2021	Julian Day	0.008	0.002	3.8	P < 0.001	6.4	14,575	14.1	0.001

Fig. 5. Mean spawning date between 1997 and 2021 for Patagonian toothfish at South Georgia. Grey solid line shows the mean spawning date for each year of the time series. Linear models added to different parts of the time series corresponding to different fishing season start dates: 1997 to 2021 when fishing commenced earlier (black) and 1999 to 2021 when fishing commenced later (red).

spatial and temporal variability of toothfish reproductive dynamics at South Georgia.

4.1. Temporal spawning patterns

Previous evidence suggested that the spawning of toothfish at South Georgia occurred over a protracted season between April and August/September (Agnew et al., 1999; Everson and Murray, 1999; Evseenko et al., 1995; Kock and Kellermann, 1991). Although, based on detailed data from a single season (1998), Agnew et al. (1999) suggested that there was a major peak in spawning in July/August, with an early peak in April. Our data also shows evidence of a peak in April. However, data for this period is limited to 1997 and 1998, when the start of the fishing season started early. A dual-peak in spawning has been reported for toothfish on the Patagonian shelf (Boucher, 2018; Laptikhovsky et al., 2006). Indeed, other notothenioid species exhibit similar spawning patterns with possible dual peaks and protracted spawning events (Everson et al., 2001); although evidence for protracted spawning is based on limited data. Brigden et al. (2017) suggested that the average spawning date had shifted later in the season and the duration of spawning reduced in South Georgia toothfish. However, their analyses did not account for the bimodality of spawning, as evidenced in the catch data pre-1999 (Fig. 4a) and made no reference to the effect size (the magnitude of the correlation) of their analyses. Our results show that whilst a statistically significant shift in mean spawning date was detected, the effect of this shift was minimal and corresponded to a shift of less than a day over the 25-years of data examined.

At a fishery level, our data clearly support existing evidence (Clark and Agnew, 2009) that catch rates and CPUE decline when toothfish are spawning at South Georgia. This is an uncommon pattern for fisheries that overlap with spawning populations, which often exhibit elevated CPUE values (Beets and Friedlander, 1999; Erisman et al., 2011). At South Georgia, this decline is most evident towards the end of July, a week immediately following the peak in the proportion of spawning toothfish in the catch (Fig. 4). Specific causes of this are unclear. However, such a decrease in the propensity of fish to 'take' baited hooks suggest that diet suppression could be playing a role, with fish not

feeding due to reduced body cavity volume because of space being occupied by eggs in females and enlarged testes in males reducing the volume available for prey within the body cavity, as has been observed in Arctic cod (*Boreogadus saida*) (Hop et al., 1995). This decline could also be due to changes in behaviour and/or changes in horizontal and vertical distribution during spawning.

4.2. Spawning hotspots

Previous investigations with a coarse resolution suggested that localised spawning occurred on several shelf break regions around the South Georgia archipelago (Söeffker et al., 2014b). These areas were then later reidentified at a finer resolution by Brigden et al. (2017). Our results, that utilise an additional 7 years of data, reaffirm the findings from both previous studies and show that statistically significant hotspots of Patagonian toothfish spawning occur in localised regions along the shelf break at both South Georgia and Shag Rocks. However, most catches did not correspond to a spatially significant aggregation. The spatial characteristics of these spawning clusters differ from those reported at the both the Falkland Islands (Brown et al., 2013; Laptikhovsky et al., 2006) and the Kerguelen Plateau (Lord and Duhamel, 2006), where, toothfish display a singular distinct spawning region. Our results suggest that such large-scale, highly localised spawning does not occur at South Georgia, which is comparable to other toothfish populations south of the Polar Front (Gon and Heemstra, 1990; Williams and Tuck, 2002). This lack of a singular spatial aggregation in toothfish populations south of the Polar Front contrasts with other related high latitude species, notably icefish (*Neopagetopsis ionah*), which are known to exhibit nesting and brood guarding behaviour with the largest known aggregation being in excess of 60 million nests (Purser et al., 2022). This behaviour creates highly aggregated populations and would increase vulnerability to focused fishery pressure and highlights the need to protect vulnerable life history stages.

At South Georgia significant spawning occurs over a series of four main hotspots around the shelf-break of the archipelago; these are: (i) West Shag Rocks region; (ii) West Gully region; (iii) to the west of the Northern BCA; and (iv) on Southern shelf-break north of the Southern
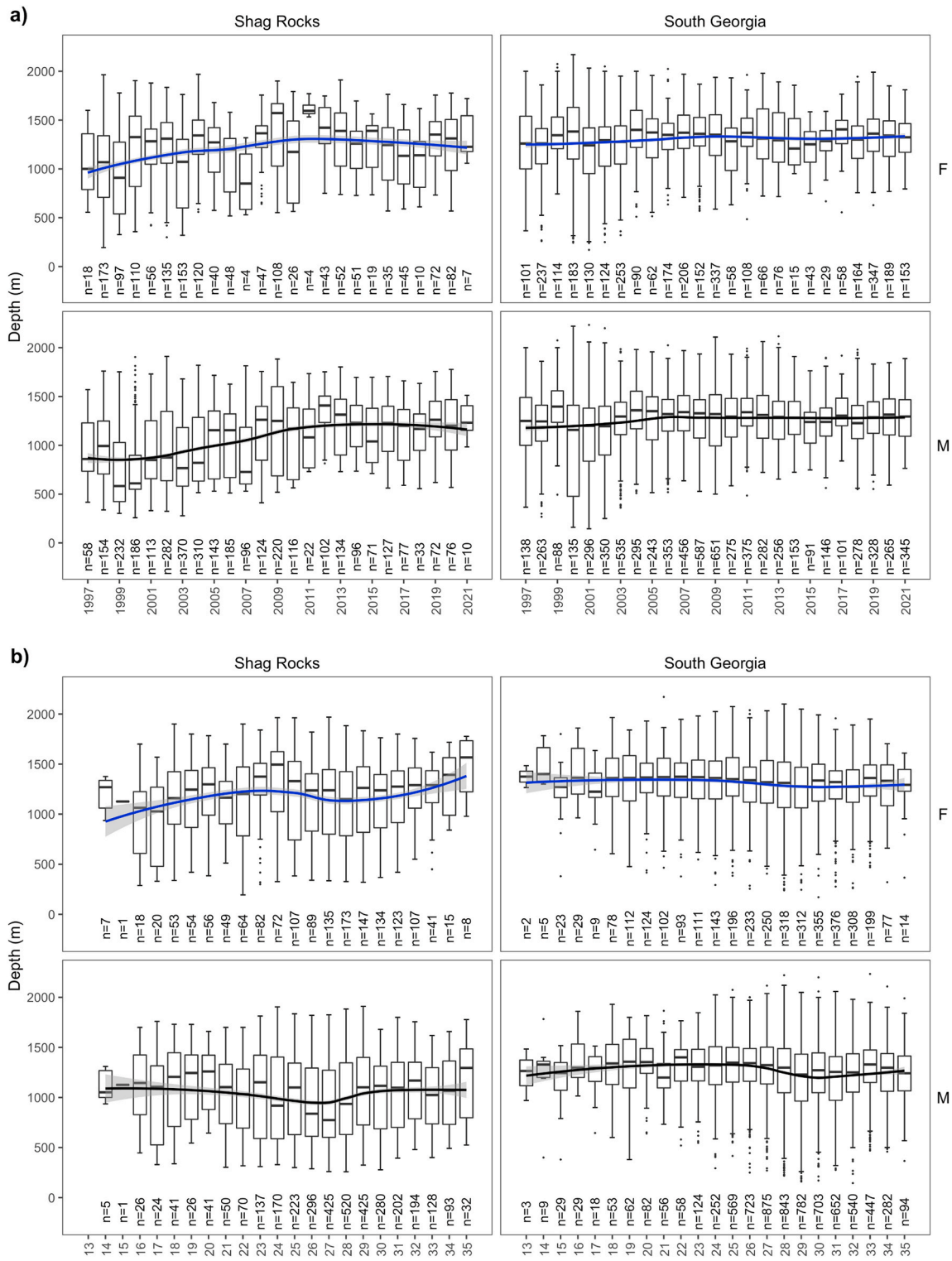
Fig. 6. Variation in catch depth characteristics for individual stage 4 spawning Patagonian toothfish (a) by year, and (b) by week for the 25-year times series between 1997 and 2021. The top and bottom tails of the boxplot represent the highest and lowest values, respectively. The top and bottom of each box represent the upper and lower quartiles, respectively, with the median value represented by the horizontal black line. Outliers depicted by dots outside of but in line with the tails. Loess smooth added to the plots, blue for female fish, black for males. Grey shading indicates ±1 standard error.

BCAs. At these hotspots, we observed a high degree of agreement between the sexes (Fig. 9).

The location of these hotspots, notably the West Shag and West Gully hotspot has previously been attributed to the influence of ocean currents (Brigden et al., 2017). These circulatory regimes influence ocean productivity (Young et al., 2011), and enhance on-shelf retention (Young et al., 2012). Here we highlight additional hotspots that also can also be explained, at least in part, by their proximity to regional oceanic currents. South Georgia sits within a highly dynamic region of the Southern Ocean and is positioned between the flows of the Polar Front to the north, and the Southern Antarctic Circumpolar Current Front (SACCF) to the south and east. Of these two fronts, the SACCF interacts with the
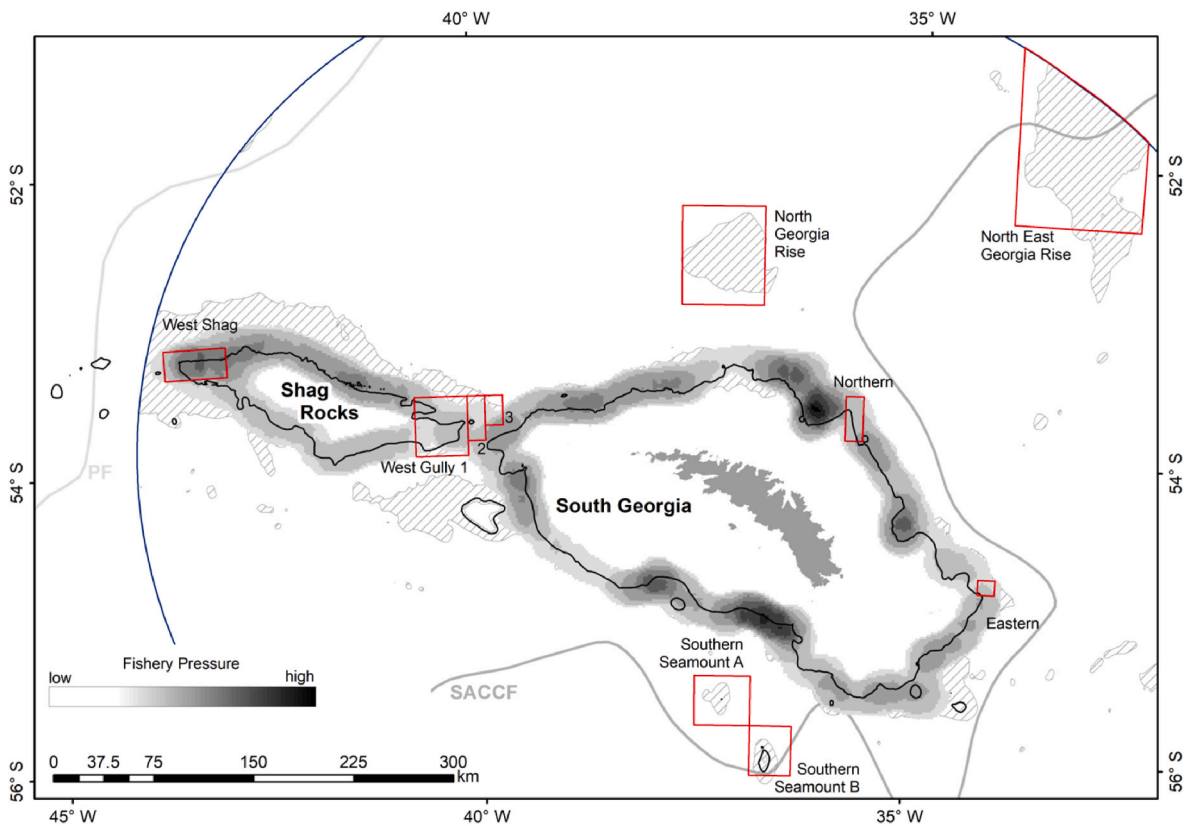
Fig. 7. Longline fishing activity at South Georgia between 1997 and 2021. Greyscale heatmap shading indicates the spatial intensity of the number of hooks set, where white indicates $<5 \times 10^3$ hooks, and black $>7 \times 10^4$ hooks per km^2. Benthic closed areas indicated by red boxes; grey hashed regions indicates the bathymetric range where the longline fishery is permitted to operate between 700 m and 2250 m; black line demotes the 1000 m bathymetric contour; light grey line labelled PF demotes the position of the Polar Front, and the darker grey line labelled SACCF denotes the position of the Southern Antarctic Circumpolar Current Front (Orsi et al., 1995; Trathan et al., 2000).

Table 4

Getis-Ord Gi* statistics for hotspot analyses carried out on spawning Patagonian toothfish caught in the South Georgia fishery between 1997 and 2021. All data were analyses in (i), for each sex (ii and iii); for each available month (iv to viii); and in five-year periods (ix to xiii), along with a single analysis on all available data (xi).

	Analysis data	n	Global G	Expected G	Variance	P	Standard deviate
i	all data	109,624	0.0009	0.0007	1.82×10^{-11}	P < 0.001	43.4120
ii	Female	57,877	0.0025	0.0021	5.09×10^{-10}	P < 0.001	17.3810
iii	Male	51,747	0.0013	0.0010	5.58×10^{-11}	P < 0.001	42.9820
iv	April	5719	0.0416	0.0416	4.16×10^{-2}	0.0416	3.1602
v	May	31,074	0.0091	0.0086	2.15×10^{-8}	P < 0.001	3.4913
vi	June	29,474	0.0036	0.0031	1.47×10^{-9}	P < 0.001	13.1180
vii	July	26,026	0.0021	0.0015	2.06×10^{-3}	P < 0.001	42.0160
viii	August	17,331	0.0037	0.0030	1.44×10^{-9}	P < 0.001	16.5450
ix	period 1997 to 2001	17,885	0.0055	0.0039	4.15×10^{-9}	P < 0.001	24.5140
x	period 2002 to 2006	29,224	0.0031	0.0025	6.46×10^{-10}	P < 0.001	22.5050
xi	period 2007 to 2011	26,344	0.0035	0.0026	1.17×10^{-9}	P < 0.001	26.5040
xii	period 2012 to 2016	17,273	0.0063	0.0057	7.14×10^{-9}	P < 0.001	7.3297
xiii	period 2017 to 2021	18,898	0.0044	0.0037	2.41×10^{-9}	P < 0.001	13.3120

Table 5

Number of detected hotspots >95% significance that occur within the Benthic Closed Areas (BCAs) over the periods before and after the establishment of the BCAs and the introduced spatial biases in data acquisition.

	1997 to 2007 (pre-BCA establishment)	2008 to 2021 (post-BCA establishment)
N of hotspots >95%	1421	1298
N within BCAs	564	79
Percentage	39.7	6.1

shelf of the island, flowing anticyclonically around the south of South Georgia, proceeding part-way along the northern shelf before retroflecting to the north-east of the island (Meredith et al., 2003; Orsi et al., 1995; Thorpe et al., 2002). Along this path, the SACCF creates on-shelf near-surface flows, which aid shelf-water retention by pushing water onto the shelf. The location of spawning in these regions may be explained by considering that eggs and larvae are greatly influenced by ocean currents, and thus any environmental advantage that aids in their retention, and thus survival, would be selected for. This is particularly key given that spawning occurs during the Austral winter (Fig. 2; Agnew et al., 1999; Everson and Murray, 1999; Evseenko et al., 1995; Kock and
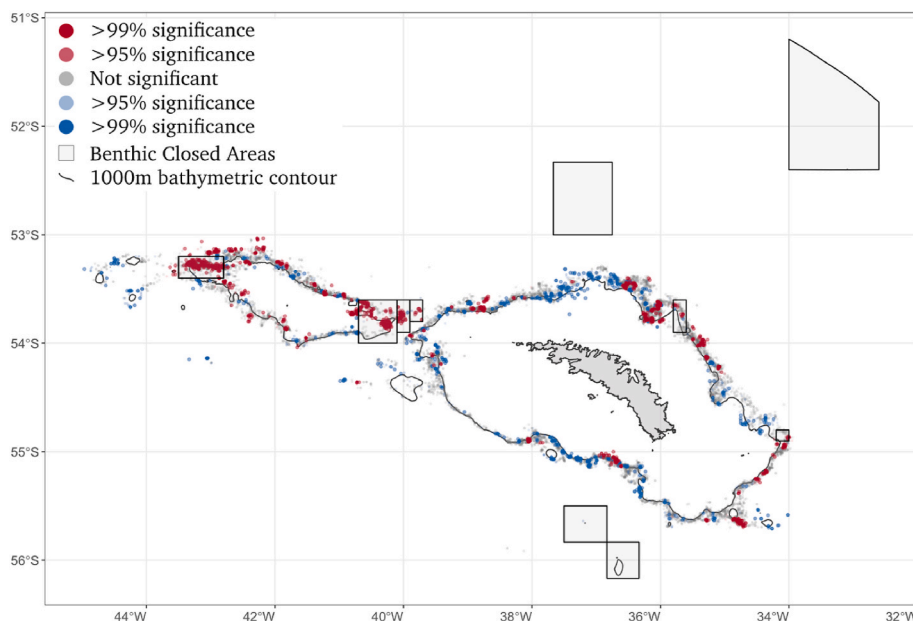
Fig. 8. Getis-Ord Gi* hotspot analyses for stage 4 spawning Patagonian toothfish at South Georgia based on all data between 1997 and 2021 (n = 15,719). Spawning hotspots are coloured red, and coldspots blue. Darker colours indicate a >99% significance, with a lighter shading indicating >95% significance. Grey dots indicate an absence of spatial clustering. Grey shaded and black bounded boxes show the Benthic Closed Areas, and the black line indicates the 1000 m bathymetric contour.

Kellermann, 1991), when off-shelf transportation is typically stronger (Young et al., 2014). Another possible explanation for the location of these spawning hotspots is evidenced at Shag Rocks, where juveniles may benefit from reduced predation rates and an abundance of prey species, notably yellowfin notothen (*Patagonotothen guntheri*) in this location (Belchier and Collins, 2008; Collins et al., 2007, 2008). This was first suggested in Brigden et al. (2017), although the extent to which this remains true for hotspots elsewhere around South Georgia remains unknown.

4.2.1. Monthly spawning consistency

The occurrence of spawning hotspots appears to be spatially consistent through the season, with major hotspots persisting throughout the winter months (Fig. 10), albeit with spawning less intense in April through June. Early in the season, there were sporadic instances of spawning on the western side of the archipelago. However, April's results were non-significant; this was likely due to low sample size, low levels of spawning and a dispersed catch during this month, lowering the sensitivity of the analyses. Additionally, during April and May spawning individuals comprised just 3.17% and 3.19% of the catch, respectively. In June, spawning fish account for 10.51% of the catch in the fishery, and with this increase in their proportion of the catch, we also see the instance of non-aggregated spawning increasing island-wide (blues, Fig. 10). July displays the most significant spawning activity, where 32.78% of the catch were stage 4 spawning fish. This is in line with the accepted peak in spawning for this species (Agnew et al., 1999; Brigden et al., 2017).

4.2.2. Inter-year spawning consistency

We analysed the catch data in five 5-year tranches to investigate inter-year spawning consistency. In doing so, we observed that inter-period spawning is consistently observed at the two major hotspots identified in Brigden et al. (2017), which were to the west of Shag Rocks and within the West Gully, particularly in the earlier periods examined (Fig. 11).

We also show that from 2002, two additional hotspots (i) the northern hotspot (~36.5°W); and (ii) the southern hotspot (~37°W) occur and persist between the later modelled periods. Separate from these major multi-year hotspots, there appears to be localised sectors of

the shelf-break on which significant spawning activity arises in one period and then decreases or is absent in another. These include isolated instances along the north-western shelf-break of South Georgia; regions along the south-eastern shelf-break, south of the Eastern BCA; and clusters along the south-western shelf-break between the West Gully BCA and the major persistent hotspot on the southern shelf-break. Inter-year variations in the prevalence of hotspots within BCAs likely stems from a knock-on impact on data availability after the establishment of the BCAs, in which fishing was highly restricted, rather than a true biological signal (Table 6).

4.3. Environmental patterns

Sea surface temperature was shown to have a significant positive correlation with sCPUE for female toothfish but a non-significant, negative correlation for males. This could be related to the earlier maturation of males compared to females (Collins et al., 2010) and that later months are linked to the gradual cooling of ocean temperatures as the season progresses. This could also be amplified by a reduced propensity to take baited lines during spawning and that females do not exhibit full maturity until they on the verge of spawning. The depth at which spawning toothfish were caught has displayed a deepening trend over the examined time series, and whilst there is the possibility that there might be a biological driver behind this, this is likely attributed to the systematic shift in fishing effort through time in response to the gradual introduction of protective management to the fishery and a reduction in the operation freedom seen in its earlier years.[1] In 2004, the minimum depth that the longline fishery was allowed to operate was 500 m. This depth limit was then amended in 2009, with a shift to a minimum of 550 m and then again in 2011 with a shift to 700 m and a maximum depth of 2250 m implemented in 2012 (Table 6). The main aim of the minimum depth limit was to reduce the catch of smaller toothfish, which are known to predominate in shallower waters, with toothfish adhering to the bigger: deeper trend (Coggan et al., 1996;

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[1] N.B. Night setting requirements came into effect from 1995 onwards (see Collins et al., 2021), so was in place for the entire duration of the timeseries analysed in this paper.
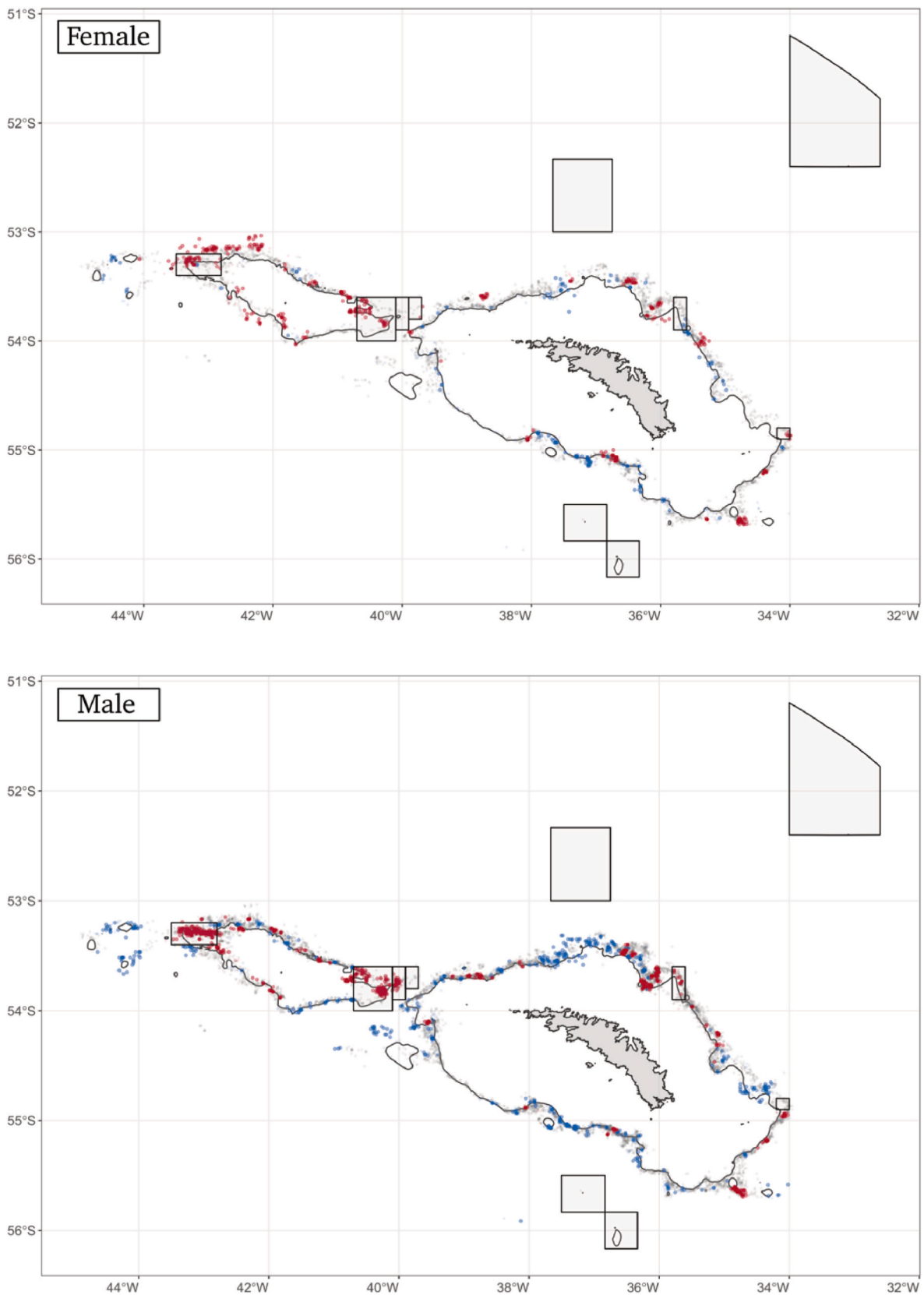
Fig. 9. Getis-Ord Gi* hotspot analyses for female (top) and male (bottom) stage 4 spawning Patagonian toothfish at South Georgia based on all available data between 1997 and 2021. Female sample size was 5,025, and males was 10,694. Spawning hotspots are coloured red, and coldspots blue. Darker colours indicate a >99% significance, with a lighter shading indicating >95% significance. Grey dots indicate an absence of spatial clustering. Grey shaded and black bounded boxes show the Benthic Closed Areas, and the black line indicates the 1000 m bathymetric contour.
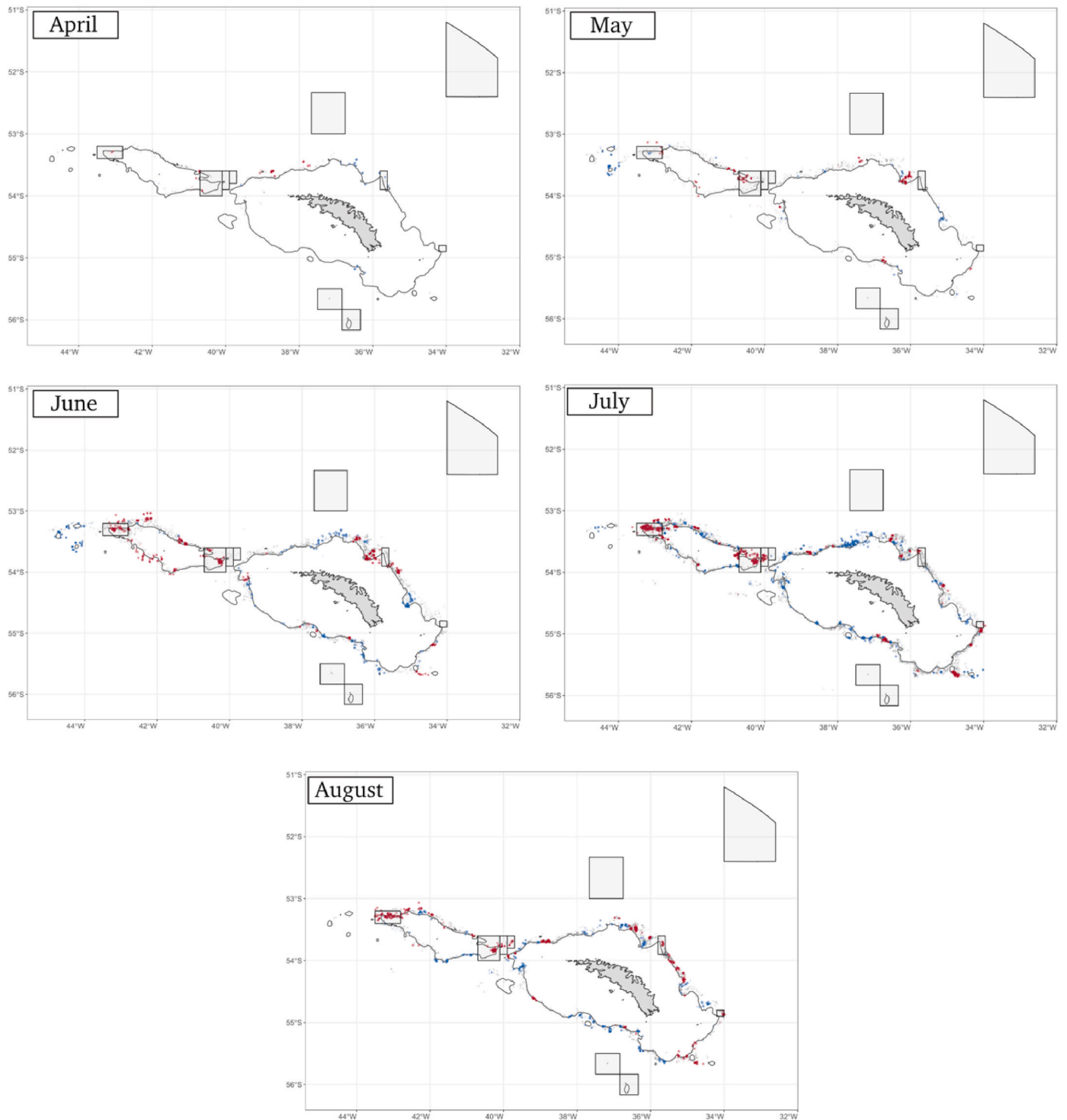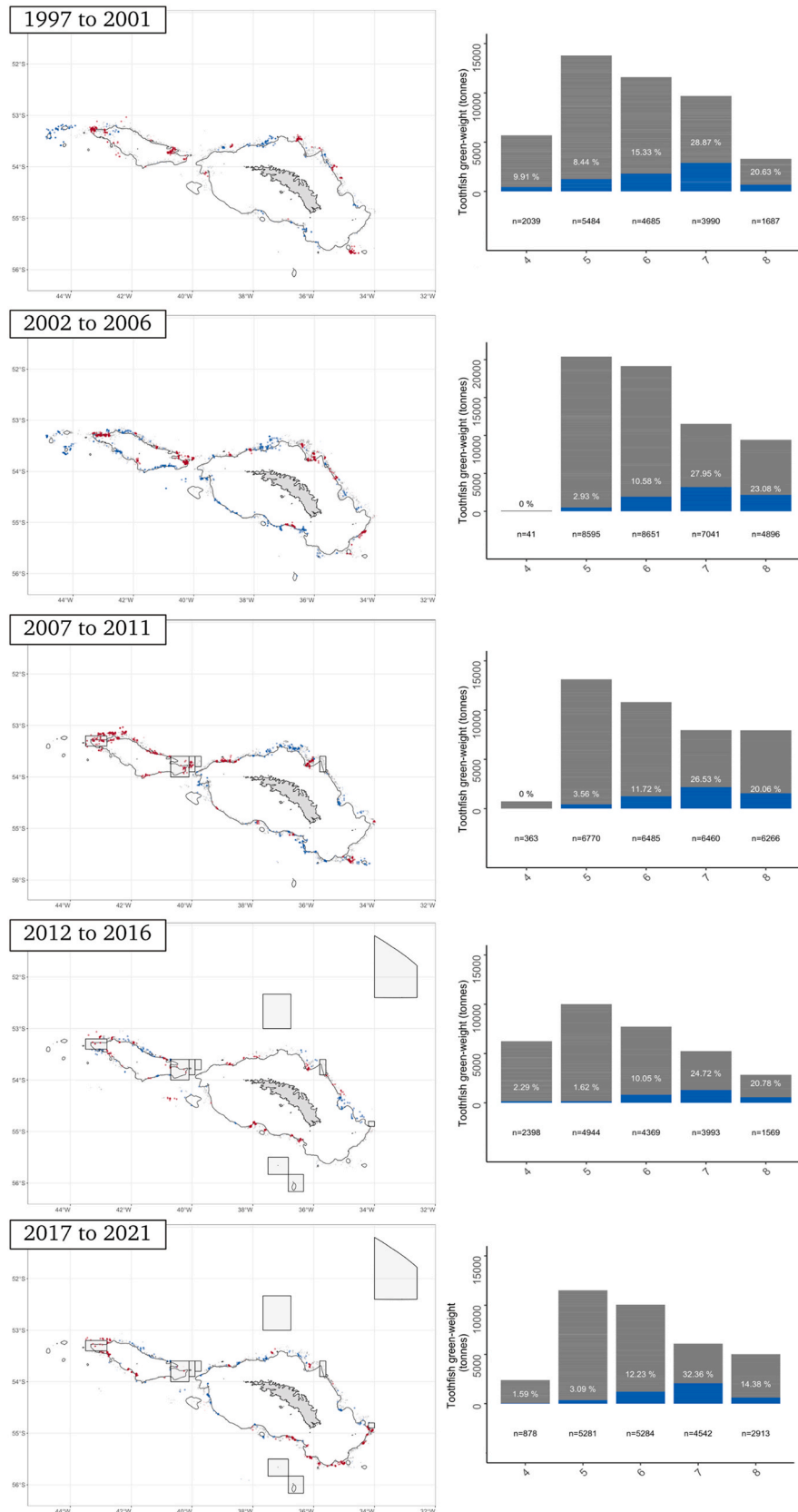
Fig. 10. Monthly Getis-Ord Gi* hotspot analyses for stage 4 spawning Patagonian toothfish at South Georgia. Monthly sample sizes are as follows: April 271; May 1199; June 3478; July 7291; and August 3480. Spawning hotspots are coloured red, and coldspots blue. Darker colours indicate a >99% significance, with a lighter shading indicating >95% significance. Grey dots indicate an absence of spatial clustering. Grey shaded and black bounded boxes show the Benthic Closed Areas present since 2007, and the black line indicates the 1000 m bathymetric contour.

Collins et al., 2007; Laptikhovsky et al., 2006; Lord and Duhamel, 2006) that is typical of scavenging fish (Collins et al., 2005). The fishery now operates in regions where catch is presumed to be reliable, which co-incides with a shift towards deeper waters.

4.4. Limitations

Spatial analyses can only be as accurate as their data. Catch data faces some noteworthy limitations. For example, it is assumed that a stage 4 gravid/ripe fish were caught on their spawning grounds, but it is possible that spawning fish were simply caught enroute, and that the inferences made about the location of spawning hotspots hold a degree

Fig. 11. Getis-Ord Gi* hotspot analyses for stage 4 spawning Patagonian toothfish at South Georgia for each of the five examined periods; sample sizes are as follows: 1997 to 2001: 2883; 2002 to 2006: 4265; 2007 to 2011: 3972; 2012 to 2016: 1887; and 2017 to 2021: 2712. Spawning hotspots are coloured red, and coldspots blue. Darker colours indicate a >99% significance, with a lighter shading indicating >95% significance. Grey dots indicate an absence of spatial clustering. Grey shaded and black bounded boxes show the Benthic Closed Areas (in the periods they applied), and the black line indicates the 1000 m bathymetric contour. Sub-plots depict the catch from April to August for the fishery with the stage 4 spawning component of the catch in shown in blue.

Table 6
Timeseries detailing shifts in the fishing season and when each of the Benthic Closed Areas and depth restrictions were implemented within the South Georgia Fishery. Shading indicates when the BCA or depth restriction was implemented.

Benthic Closed Area / management measure	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021
West Gully												▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓
West Gully Extra												▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓
West Shag												▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓
Northern												▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓
Southern Seamounts												▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓
Eastern												▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓
NE Georgia Rise												▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓
Minimum depth (m)								500	500	500	500	500	500	550	700	700	700	700	700	700	700	700	700	700	700
Season dates	01-Mar to 31-Aug	01-Apr to 31-Aug	15-Apr to 31-Aug	01-May to 31-Aug	01-May to 31-Aug	01-May to 31-Aug	01-May to 31-Aug	01-May to 31-Aug	01-May to 31-Aug	01-May to 31-Aug	01-May to 31-Aug	01-May to 31-Aug	01-May to 31-Aug	01-May to 31-Aug	01-May to 31-Aug	01-May to 31-Aug	01-May to 31-Aug	16-Apr to 31-Aug	16-Apr to 31-Aug	16-Apr to 31-Aug	16-Apr to 31-Aug	16-Apr to 31-Aug	01-May to 31-Aug	01-May to 31-Aug	01-May to 31-Aug
Season extensions or trials*	None		Line weighting trials in February	None			Conditional extension from 16th April	Conditional extension to 14th September						Conditional extension from 26-Apr and to 14-Sep	Conditional extension from 21-Apr and to 14-Sep	Conditional extension from 16-Apr and to 14-Sep	Conditional extension from 11-Apr and to 14-Sep	Conditional extension from 06-Apr and to 14-Sep	Conditional extension to 14-Sep						

of spatial inaccuracy. A further assumption relates to the Kock and Kellermann (1991) maturity scale applied by the CCAMLR observers. This scale aggregates ripe and gravid fish, but does not explicitly define running fish as a stage as is found in more detailed maturity scales, for instance those adapted from Nikolsky (1963). In this instance, however, the implementation of the Kock and Kellermann (1991) scale is justified due to its relative simplicity of use for shipborne observers and the fact that the difference between gravid/ripe to running fish is not well defined for toothfish.

Another assumption relates to how representative the sample is of the population and whether identified hotspots correspond to wider population-level activity. However, given the temporal consistency of the detected spawning areas, and the size of the data set utilised here, the potential bias is likely minimal. To further mitigate against these limitations systematic tag deployment can offer a means of long-term spatial and population level monitoring (Söeffker et al., 2014a, 2014b). Additionally, observational surveys, such as camera traps (e.g. Collins et al., 2006; Yau et al., 2001) or biologging (e.g. Brown et al., 2013) could be conducted to observe behaviour *in situ* and validate the catch-based predictions. However, these have historically lacked scalability, although technological advances are enhancing capacities here (Lowerre-Barbieri et al., 2019). Another caveat of the data analysed here is that due to the random sub-sampling strategies employed by the CCAMLR observers as a matter of necessity, biological data (*i.e.*, sex, maturity, length, weight, *etc.*) are only available for a subsample of the total catch. These data are also dependent on individual observers' interpretation and consistent implementation of protocols, including maturity scales. Here, we employed a simple, yet effective method to produce comparable CPUE estimates between maturity stages and was individual to each sex and line set throughout the 25-year timeseries.

The restriction of the fishery to the winter months, to minimise the risk of seabird mortality (Collins et al., 2021) limits data availability and hence, a proportion of a toothfish's life cycle remains 'unobserved' when reliant on catch data. In this instance, this limitation has restricted our ability to confirm the potential occurrence and extent of an early

spawning peak in autumn at South Georgia. Furthermore, the limitation of fishery activity to May onwards for most of the analysed time series provides an explanation of the non-significant result seen in April (Table 4). Here, the limited sample size available for April, which was one third the size of the next smallest month likely hindered the power of the HSA analyses over the large area examined. The potential benefits of exploring autumnal toothfish activity and this component of their life-cycle poses too great a risk to other species, which have suffered due to this fisheries historical seabird bycatch (Collins et al., 2021).

Finally, whilst the methods applied here are powerful in their ability to detect spatial patterns in large volumes of data, one thing they do not attempt to explain is the underlying drivers of the observed patterns. Here we discuss possible environmental drivers of the observed hotspots, but these are likely influenced by a complex suite of variables which it was beyond the scope of this study to investigate. This would be an interesting avenue to explore in the future, for instance by following similar approaches implemented on this species elsewhere in the Southern Ocean (e.g., Péron et al., 2016). The results of such a future study would be beneficial informing future adaptive management for this species in this region.

4.5. Spawning and management overlaps

At South Georgia, toothfish fishing is carefully managed with strict catch limits, various technical measures and a significant closed season which concentrates fishing in the period around and during the spawning months. Our results show that whilst there are hotspots of spawning, there is no single area where concentrated spawning occurs at South Georgia, which differs from those that are observed on the Patagonian shelf and Kerguelen Plateau, where spawning is more easily delineated (Brown et al., 2013; Laptikhovsky et al., 2006; Lord and Duhamel, 2006).

The BCAs (formally reduced impact areas) were implemented from 2008 onwards (Fig. 1) and, whilst primarily designed to protect vulnerable marine ecosystems (VMEs, Trathan et al., 2014), they show a

high degree of overlap with the detected spawning hotspots (Table 7). At their present extent the BCAs cover approximately 15% of the permitted fishing area (700 m–2250 m; Trathan et al., 2014). Our analyses show that pre-2008, when the BCAs were introduced, 39.7% of the detected hotspots of >95% significance occurred in areas where the BCAs were subsequently established. This demonstrates that a high degree of overlap between spawning areas and the BCAs exists, and whilst none of the BCAs refer to toothfish spawning in their management remit, incidental protection is present. However, an important aspect to note here is that since 2008, all fishing within these BCAs has been prohibited (with the exception of tag-deployments in support of the toothfish stock assessment), and as such, from 2008 onwards the observed trend that hotspots are diminishing with the BCAs is an artefact of the lack of data collection (i.e. reduced fishing) and is not an indication that spawning itself is reducing in a region; these patterns are visually evident in more recent years (Fig. 11). Consequently, the presented overlaps between the existing BCAs and the detected hotspots are likely highly conservative in regions where data were limited.

The restriction of the fishery to winter has been entirely driven by the need to minimise seabird by-catch, with operation in different months coming at too great a risk to seabird populations (Collins et al., 2021). The season can be extended into mid-September (under CCAMLR regulations), but this has rarely been taken up. Therefore, timing options of the fishery season are limited. It is arguable whether it makes a difference to a population if fishing occurs before, during or after a spawning period, particularly when the fishery is well managed, and the exploitation rate is low, as is the case here with an exploitation rate of ~4% per year and an aim to maintain stock biomass at or above 50% of pre-exploitation levels (Earl and Readdy, 2022).

One aspect of fish biology that may mitigate the impact of harvesting is the susceptibility of the target species to being caught during spawning. However, this can be difficult to assess as it is influenced by both internal and external factors (Biggs et al., 2021; Erisman et al., 2011; Solmundsson et al., 2003). Aggregatory spawning behaviour is one such example of an internal factor, which is displayed by both shallow spawning species (e.g., multiple grouper species, *Epinephelus* spp. (Hughes et al., 2020; Sadovy de Mitcheson et al., 2020)) and deep spawning species (e.g., orange roughy, *Hoplostethus atlanticus*

(Pankhurst, 1988; Trueman et al., 2013)). Such aggregations put populations at risk from focused fishery pressure and have been linked to artificially elevated CPUE alongside declining stocks (Beets and Friedlander, 1999; Erisman et al., 2011). External pressures also act on populations, for instance for Patagonian toothfish at South Georgia, there is a notable decrease in the fishery CPUE during the July spawning peak (Fig. 4), indicating that the catchability decreases during the main spawning period. This reduced catchability could shift fishing effort elsewhere, both spatially and temporally. This could lead to the removal of non-spawning demographics, which would negatively impact future recruitment of the population (Clarke et al., 2015; Grüss et al., 2013; Grüss and Robinson, 2014). Furthermore, with less hooks taken by toothfish, there is likely to be an increase in bycatch during the spawning period.

4.6. Fishery management implications & future work

Our analyses indicates that 40% of spawning hotspots were located within the South Georgia BCAs. Three of the BCAs (West Shag, West Gully 1 and Northern) were introduced in 2008 with the West Gully extended in 2011 and Southern Seamounts and Eastern BCA added in 2013 (Table 6). Any alterations to the extent of the BCAs specifically to target protection towards toothfish spawning would have to be carefully considered to avoid spatially restricting the tagging programme (Marsh et al., 2022), on which the stock assessment is dependent and also to not adversely impact other demographics of the population.

A temporal closure that spans the known spawning season could mitigate the impact of a BCA on tag dispersal. However, there would need to be a consideration into the efficacy of spawning specific closures, particularly given the high variability and episodic nature of toothfish spawning success at South Georgia (Belchier and Collins, 2008; Collins et al., 2007, 2010). The observed recruitment cycles at South Georgia, suggest that spawning is inherently subjected to a degree of natural variability, with several years in between each successful cohort; the success of which has been inversely correlated with sea surface temperature (Belchier and Collins, 2008). This intrinsic natural variability would reduce the efficacy of a spawning-specific spatial closure as, irrespective of protection, in some years the natural environmental

Table 7

Summary of spawning activity within the extents of the shelf-break Benthic Closed Areas. (✓) indicates that there is evidence that shows that spawning occurs in the named model, and the (–) indicates that there is only evidence of spawning over a portion of the modelled period or that there is only a partial overlap with this BCA and the modelled data.

Benthic close area name	Evidence of spawning activity in:					Description
	All data model	Male model	Female model	Seasonal model	Five-year tranches	
West Shag 1039 km² Est: 2008	✓	✓	✓	✓	✓	Located on the western tip of the Shag Rocks shelf-break, our analyses show that there is a high degree of overlap under all derivations of the analyses. This region is shown to be highly significant for the spawning of both sexes, and that spawning occurs throughout the season, peaking from June to August once a period of initial variability is overcome. At this location there is also evidence for significant clustering of spawning activity throughout the time series, particularly between 2002 and 2011. The observations here are congruent with known spawning dynamics shown in Brigden et al. (2017).
West Gully (1, 2, & 3) 2236 km² Est: 2008 & 2011	✓	✓	✓	–	–	These BCAs are in a region where evidence of toothfish spawning is present and is highly significant for both sexes from May onwards. There is little spawning here during April. Throughout the examined time-series, the footprint of this BCA contains evidence of spawning activity over all examined time periods. Decreased spawning activity in later years is likely due to the introduction of the BCAs.
Northern 441 km² Est: 2008	✓	✓	✓	–	–	This BCA is located on the northern shelf-break of South Georgia, just to the east of a southerly recession of the shelf-break. This region is known to be the focus of the krill fishery in these waters (Bamford et al., 2021; Trathan et al., 2021). There is evidence that this BCA is significant for both sexes, but primarily significant later in the season (July/August). Through the time series, there is only evidence that this BCA covers significant spawning hotspots from 2002 onwards.
Eastern 143 km² Est: 2013	–	✓	✓	–	✓	This BCA is located at the are eastern end of the South Georgia shelf-break. Our analyses show that there is evidence of spawning activity on the periphery of this BCA throughout the time-series, which is reflected for both sexes. Main spawning clusters are found on the south-eastern edge of this BCA, and spawning activity appears to increase late in the season at this location. Activity at these locations is observed from 2002 onwards.

conditions are not conducive to a successful spawning, and spawning naturally fails. When this is combined with the reduction in the propensity of toothfish to take a baited line whilst spawning would further negate efforts to directly protect spawning areas. The reasons for the drop in CPUE during spawning are not clear but could be due to changes in distribution (following bathymetric contours or vertically in the water column) or a change in behaviour when gravid/ripe. A lack of feeding in spawning fish has been reported in other species (i.e., cod, *Gadus morhua*; Fordham and Trippel, 2002) and is the most likely cause of the reduction in the propensity to take baited hooks.

Although fishing, specifically trawling, has been implicated in the disruption of spawning behaviour in some fish species (Dean et al., 2012; Morgan et al., 1997; Robichaud and Rose, 2003; Sadovy de Mitcheson and Erisman, 2012), there is no evidence that longlining influences spawning. However, the inherent aggregatory spawning behaviour exhibited by toothfish, and indeed nesting behaviour exhibited by other high latitude species (i.e., ice fish; Purser et al., 2022), increases the baseline risk, by the very fact that populations are more concentrated and nests are vulnerable to focused external influences, during these stages of their lifecycle. Given this, there is a need to factor both habitat and vulnerable life history stages into future research and management plans. Another important consideration is the commensurate increase in bycatch resulting from the distinct drop in CPUE during the spawning season; this should be a focus of future analyses.

To fully understand the impact of targeting a population, there is a need to consider both lethal (i.e., the removal of fish) and non-lethal factors (i.e., the impact of lower animal numbers on the efficacy of reproduction). To further enhance the protection afforded to toothfish at a crucial stage of their life cycle, our understanding of both the temporal and environmental drivers needs developing, and with this, more targeted management can be put in place. By understanding what influences spawning location, timing, and inter-year persistence we can begin to predict how spawning scenarios may react to shifts in climatic processes. Thus, informing and providing temporal longevity to management actions, the fishery and to acting to safeguard this species into the future.

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

Data available on request to the CCAMLR Secretariat

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