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Defining the relationship between Patagonian toothfish and their environment in Subarea 48.3

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Abstract

This paper presents initial findings from a research project evaluating climate change risks to toothfish in subareas 48.3 and 48.4. Here we focus on Patagonian toothfish (*Dissostichus eleginoides*) in Subarea 48.3, using groundfish survey data to develop preliminary distribution models. Data were split into size-classes before analysis and distribution models constructed, informed by relationships with environmental covariates. Based on the expectation of ontogenetic shifts in depth range and the potential effects of temperature, we used models to estimate depth ranges, and temperature values, occupied by each size-class of Patagonian toothfish. Initial findings indicate strong inter-annual variability in juvenile recruitment at Shag Rocks, with considerably weaker recruitment on the South Georgia shelf, where juvenile abundance was lower and larger fish predominated. Over the groundfish survey time-period (1986-2023) sea surface temperatures (SST) have increased at both South Georgia and Shag Rocks, most rapidly at the former. For both locations, the rate of warming is greatest during austral spring and summer. Despite a long-term increasing trend in average SST, periods of cooler summers/autumns occurred in some years and cooler winters in others. Spatial patterns of Patagonian toothfish biomass consistently showed significant relationships with depth and mean SST, with preferences for specific depths and temperature regimes that varied by size class. We note that the long-term mean SST threshold of 1.8°C, which divides areas of high and low Patagonian toothfish abundance, aligns with the geographic division between Shag Rocks and South Georgia shelf. This suggests SST relationships may also serve as a proxy for biogeographic and/or other oceanographic factors that characterize these areas. This work provides a foundation for determining species-environment relationships across different life history stages, offering insights into important determinants of distribution, as a basis for better understanding the effects of climate change. We outline the next steps for this project and welcome input and engagement from WG-FSA.

Background

The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) has recognised the need for climate-responsive options within its ecosystem approach to management (Cavanagh & Pardo 2023). The recent CCAMLR Workshop on Climate Change (WS-CC-2023) discussed the need for fishery management measures to reduce and manage the risks from both rapid and longer-term climate change, agreeing to a set of recommendations to achieve this (SC-CAMLR-42, Annex 11; Cavanagh & Pardo 2024).

This paper presents preliminary results from a Darwin Plus (UK Government) funded project addressing this need with a focus on toothfish in subareas 48.3 and 48.4 (Cavanagh et al. 2023). Initial steps in this project have focused on Patagonian toothfish (*Dissostichus eleginoides*) in Subarea 48.3. The region is undergoing rapid climate-driven changes, including in ocean temperatures, acidification, winds, circulation, and sea ice (IPCC, 2019; 2022; Cavanagh et al. 2021). The fishery for Patagonian toothfish in Subarea 48.3 is managed in accordance with CCAMLR's assessment methods and decision rules (Earl & Readdy, 2023, 2024). However, environmental parameters are not directly included in

CCAMLR stock assessments for toothfish. There is a need to understand the impacts of environmental variability and climate change on habitat, stock distribution and productivity (Welsford 2023; WS-CC-2023), so that management decisions can account for a changing environment. For example, climate change risks may be higher for certain stocks and areas than others based on life history and exposure to change.

Establishing a detailed understanding of target species, including their life histories, in relation to their environment is essential for effective fisheries management in the face of climate change. The recent Climate Change Workshop emphasised the importance of considering all life stages. Each life-stage will have different sensitivity and exposure to changing environmental conditions due to factors including physiology (e.g. thermal tolerance), distribution (including ability to disperse) and trophic position (Freer et al. 2019).

The distribution of toothfish during their life-history stages and the ontogenetic migrations they undertake determines the environmental conditions to which they are exposed. Patagonian toothfish in this region are considered to be a single, mostly self-contained population that complete their life cycle within subareas 48.3 and 48.4 with minimal connectivity to other populations (Rogers et al. 2006; Shaw et al. 2004; Soeffker et al. 2022). Patagonian toothfish spawn annually in the austral autumn and winter, typically on the South Georgia-Shag Rocks shelf-margin with evidence of some hotspots of spawning (Bamford et al. 2024). Pelagic eggs drift passively from spawning grounds, hatching into pelagic larvae capable of some directed movement. The majority of Patagonian toothfish larvae (only 43 reported) have been caught in surface waters to the northwest of South Georgia (North, 2002). Juveniles are primarily found on the continental shelf near Shag Rocks at depths of 100-300m, undertaking an ontogenetic downslope migration as they grow (Collins et al. 2010). The result is an age-structured distribution by depth with maturing and adult fish more commonly found at depths between 700-2000m (Brigden et al 2017; Bamford et al. 2024). There is some movement between subareas 48.3 and 48.4 (Figure 1), which appears to be immature fish migrating to 48.4, perhaps in periods of good recruitment (Soeffker et al. 2022). There is no evidence of spawning in 48.4, with adults migrating back to the South Georgia and Shag Rocks shelves to spawn (Soeffker et al. 2022).

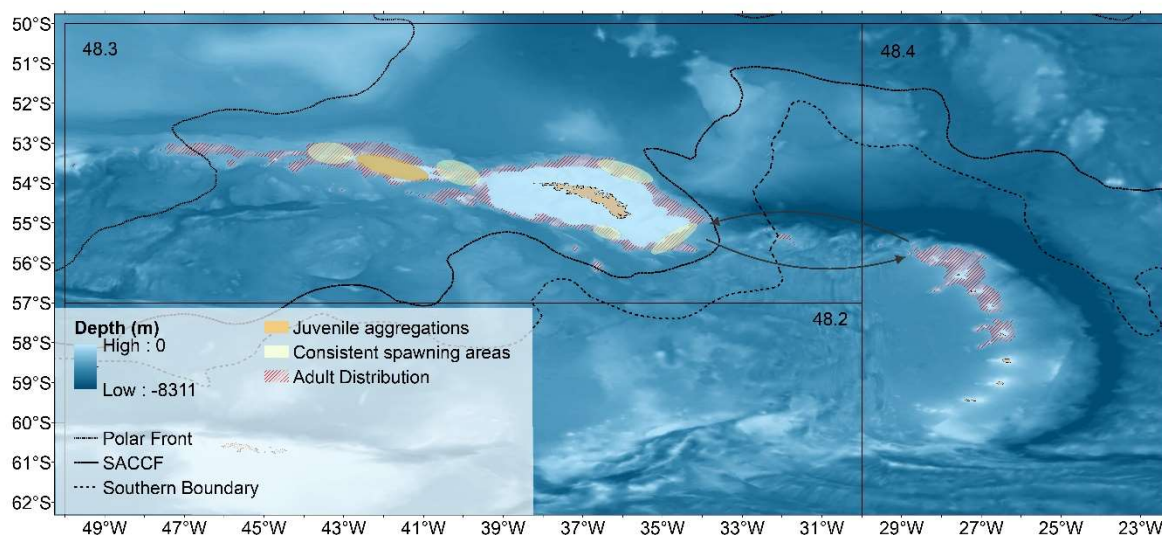


Figure 1. The location of suspected nursery (orange shaded ellipse) and spawning (yellow shaded ellipses) habitats are approximated from the cited literature (Belchier & Collins, 2008; Bamford et al. 2024). Habitat of adult Patagonian toothfish is shown in the red hatched area (500 - 2000m). The distribution of the key habitats are shown in relation to oceanographic features and fishery management areas. The extent of CCAMLR Area 48 and the Subareas are shown in black boxes. The mean positions of the Polar Front (PF), South Antarctic Circumpolar Current Front (SACCF), and Southern Boundary of Antarctic Circumpolar Current Front (SB) were calculated using satellite data from 1993-2012 (Park and Durand 2019). Known connectivity between habitat areas is highlighted by grey arrows.

Changes in ocean temperature may affect the planktonic duration, development and survival of eggs and larvae. This is predicted to affect dispersal patterns, which may in turn affect the ability of fish species to adapt to ongoing environmental change (IPCC, 2019). Toothfish eggs and larvae are planktonic, occurring in surface and shallow waters (North, 2002) meaning they are more likely to be susceptible to changes in sea surface temperature (SST) than later life stages. Growth and survival are likely to be influenced by environmental conditions including temperature and acidity. On-shelf retention resulting from the oceanic circulation is likely to be important for recruitment into the juvenile stock.

The distribution of adult toothfish appears to be constrained by factors including depth and temperature. They occur in deeper waters with bottom temperature being more relevant to this life stage than SST. The lack of antifreeze proteins in *D. eleginoides* (compared to *D. mawsoni*) may limit its temperature tolerance (Collins et al., 2010; Soeffker et al. 2022). Eastman (1990) suggested a lower temperature limit of 2°C for *D. eleginoides*, although since then individuals have been observed at temperatures as low as 1.4°C (Collins et al. 2005). Most adults appear to have high site fidelity, with tagged fish often recaptured close to release location, however some fish have undertaken longer (100s of km) migrations (Soeffker et al. 2022).

There is some evidence that spawning Patagonian toothfish are sensitive to environmental variability and may skip annual spawning events in sub-optimal conditions (Everson and Murray, 1999, Brigden, 2019, Bamford et al. 2024) and skip-spawning has been reported for Patagonian toothfish in other regions (Boucher, 2018). Spawning aggregation locations have been linked to oceanographic currents that may improve prey availability and/or on-shelf retention of juveniles (Brigden et al. 2017). Little is known as to optimal/preferred spawning conditions.

Here, we present our preliminary steps and findings exploring the relationship between Patagonian toothfish and their environment, focusing on groundfish survey data from Subarea 48.3. This work provides a foundation for determining species-environment relationships across different life history stages, offering insights into important determinants of distribution, as a basis for better understanding the effects of climate change and what this means for management.

Methods

Study region

While the study region for the project encompasses subareas 48.3 and 48.4, for this paper, we present initial analyses and findings for Subarea 48.3, specifically South Georgia and Shag Rocks. A deep-water canyon (depth ranging from ~1,600m to 2,000m) separates these two shelf regions, with overall warmer conditions and proximity to the Polar Front at Shag Rocks, and surface influx of cold freshwater on the South Georgia shelf from glacial run off.

Data

All analyses and data processing were performed in R version 4.3.3 (R Core Team 2024).

Trawl surveys

Data on Patagonian toothfish distribution were collected during 28 groundfish surveys conducted approximately biennially on the South Georgia and Shag Rocks shelves (Subarea 48.3) between 1986 and 2023 (see Annex Table A1). Sampling methods have been consistent over time, consisting of 30-minute demersal trawls (with a 120-foot otter trawl, with wingspread 18–20m, headline height 3–6m,

cod end mesh of 40mm; Belchier et al. 2015) carried out during daylight (between nautical twilight at dawn and dusk) at a ship speed of ~3 knots. Surveys were predominantly undertaken during the austral summer (November-February), except for 1997 and 2007 (August-September), 2008 (April), and 2021 (May; see Annex Table A1). For each trawl, total toothfish weight was recorded in addition to depth, distance, and horizontal wingspread. Prior to analysis, trawls that were unrepresentative (gear failure, unsuitable ground, duration < 15 minutes) were omitted. Surveys encompassed the continental shelves of South Georgia and Shag Rocks, with greatest sampling effort to the NW of South Georgia and on the Shag Rocks shelf (see Hollyman et al. 2021).

Size distribution and construction of size-classes

During each trawl, the majority of toothfish caught were measured (total length; cm) and weighed. Using these size distribution data, the relative strength of age group cohorts and the size limits separating those age groups were identified. We identified six size-classes as a proxy for ages 1+ to 6+ (or adult) fish based on discrete modes represented in size distributions among years (Table 1), guided by known growth rates in juvenile Patagonian toothfish (~100-120mm per year; Collins et al. 2010) and confirmed via Gaussian mixture model analysis using the mixR package in R (Yu 2021).

Table 1. Size-classes applied to Patagonian toothfish (*Dissostichus eleginoides*) records as a putative measure of age-groups.

Size class	Age	Size range (cm)
1	1+	≤ 25
2	2+	26 – 37
3	3+	38 – 47
4	4+	48 – 57
5	5+	58 – 66
6	6+	> 66

The total catch weight for each trawl was then sub-divided into size-class specific catch totals by summing individual fish weights in each size-class, providing trawl-specific measures of overall catch weight (kg) and catch weight by size-class. Catch per unit effort (CPUE; kg km⁻²) is presented either as an overall value or by size-class, calculated using a swept area approach (Hollyman et al. 2021) with effort equal to the area covered during deployment (trawl distance × wingspread; km²). To indicate changes in overall and size-class specific density through time, we calculated the mean CPUE per survey along with its 95% confidence interval calculated via bootstrap resampling (n = 1000 permutations). Given differences in CPUE, we performed these calculations based on trawls undertaken on the Shag Rocks and South Georgia shelves separately.

Sea surface temperature data and processing

SST was used as a proxy/indicator of climate variability during the groundfish survey period (1986-2023). Data were obtained from the Global Ocean OSTIA dataset archived on the Copernicus Marine Data Store (product: sst_glo_sst_l4_rep_observations_010_011; doi: 10.48670/moi-00165). Data consisted of global daily fields from 1981 to 2023 at 0.05° horizontal resolution. The gridded data fields were initially cropped to the 2000m isobath within the bounding region 53-55.7°S, 34-44°W, which was then further sub-divided at 40°W to create a set of daily fields specific to the South Georgia (east

of 40°W) and Shag Rocks (west of 40°W) shelves. These regional fields were spatially averaged to produce a time-series of daily mean SST at Shag Rocks and South Georgia. To represent long-term patterns in surface temperatures, we calculated two alternate measures of regional climate. We firstly calculated SST anomaly (SSTa) by subtracting the 30-year (1982-2011) seasonal climatology, which was constructed for each day of the year by averaging regional SST across years (1982-2011) within an 11-day window centred on the day of year in question. The resulting time-series of SSTa provides an indication of warmer/cooler periods of surface temperature conditions through time. Secondly, we calculated season-averaged SST for each year to examine seasonal warming trends. Seasons are defined by 3-month time-windows (Dec-Feb, Mar-May, Jun-Aug, Sep-Nov), providing information relevant to important life-history stages of egg (Jun-Aug, Sep-Nov) and larval dispersal (Sep-Nov, Dec-Feb) wherein individuals are in upper water layers (Collins et al. 2010).

Patagonian toothfish distribution models

Distribution models for each size-class were constructed based on catch weights recorded in each trawl across the 28 groundfish surveys informed by relationships with bathymetric and environmental covariates (**Table 2**).

Bathymetric and environmental covariates

Bathymetry data were obtained from the ETOPO 2022 global relief model (NOAA 2022). Seafloor depth was used to calculate the slope of the seabed (terrain function in the raster package; Hijmans 2023). Environmental variable datasets were obtained from the Copernicus Marine Data Store (**Table 2**), and comprised daily fields of temperature, salinity, current magnitude, and ocean chemistry (dissolved O₂ and NO₃ concentrations) at the surface and near the seabed, and eddy kinetic energy (EKE), mixed layer thickness (MLT) and surface chlorophyll-a (chl-a) concentration (**Table 2**). Spatial resolution of the environmental datasets ranged from 0.05° to 0.25° (**Table 2**). Average climatological mean and variability (standard deviation) fields for each environmental variable were calculated on a cell-by-cell basis.

Values for each bathymetric and environmental variable were then assigned to trawls according to trawl mid-point location. Several measures of variability (currents, chlorophyll-a, DO₂ and NO₃) were excluded at this stage to avoid collinearity as they were highly correlated ($r = 0.9-0.98$) with the climatological mean of the same variable.

Table 2. Trawl-specific and environmental covariates, data sources, and processing information for variables included in Patagonian toothfish distribution models.

Variable	Description	Source	Time-range	Resolution
survey	Survey categorical variable			survey
date	Survey mid-point date			survey
sun	Sun altitude above the horizon (radians)			trawl
area_km2	Area swept during trawl in km ²			trawl
depth ^a	Depth	ETOPO 2022		0.0167°
slope	Seafloor slope			
SST.mean	Mean sea surface temperature	Global Ocean OSTIA SST ^b	1981- 2023	0.05° daily
SST.sd	Variability (SD) of sea surface temperature			
SSal.mean	Mean sea surface salinity	Global Ocean Physics Reanalysis ^c	1993- 2023	0.083° daily
SSal.sd	Variability (SD) of sea surface salinity			
FTemp.mean	Mean temperature near seafloor			
SVel.mean	Mean surface current speed			
EKE.mean	Mean eddy kinetic energy			
MLT.mean	Mean mixed layer thickness			
CHL.mean	Mean surface chlorophyll-a concentration	Global Ocean Colour ^d	1997- 2023	4 km daily
FDO2.mean	Mean dissolved oxygen (DO ₂) near seafloor	Global Ocean Biogeochem. Hindcast ^e	1993- 2023	0.25° daily

a: In-situ depth measurements were used in model fitting, with bathymetry data used to predict distributions.

b: Copernicus Data Store (product: sst_glo_sst_l4_rep_observations_010_011; doi: 10.48670/moi-00165)

c: Copernicus Data Store (product: global_multiyear_phy_001_030; doi: 10.48670/moi-00021)

d: Copernicus Data Store (product: oceancolour_glo_bgc_l4_my_009_104; doi: 10.48670/moi-00281)

e: Copernicus Data Store (product: global_multiyear_bgc_001_029; doi: 10.48670/moi-00019)

Distribution model framework

For each size class (response: size-specific catch weights) and overall (response: total catch weight) Patagonian toothfish catch, we constructed distribution models using generalized additive models (GAMs; Wood and Augustin 2002) given the likelihood of non-linear relationships between spatio-environmental factors and toothfish distribution. In all cases we used a Tweedie (tw family, log-link) distribution given that catch weights were measured on a continuous scale, but with a mass at zero corresponding to trawls where no fish (or fish in that size-class) were caught (Lecomte et al. 2013). Models were estimated using gam in the mgcv package in R fitted via restricted maximum likelihood (REML; Wood 2011).

Several model components were included in every model to account for differences through time and among trawls within a survey. A smooth for date and survey random effects were specified to account for potential long-term trends and interannual variability among surveys, respectively. Time of day was also included via a smooth based on sun altitude ($x = 0$ at dawn, $x = \pi/2$ at zenith) to model potential diel vertical movement that may influence catch rates. We also include an offset term of $\log(\text{area-swept})$ to account for differential trawl effort, which has the effect that model predictions are equivalent to CPUE.

Spatial variability in Patagonian toothfish density was modelled via smooth terms for environmental and bathymetric covariates (henceforth collectively referred to as habitat covariates; **Table 2**). Multicollinearity among covariates was addressed by excluding one covariate from each covariate pair

with severe collinearity (correlation coefficient, $|r| \geq 0.8$), and grouping covariates with moderate multicollinearity ($0.55 < |r| < 0.8$) into sets to be trialled against each other. Depth, seabed slope, and mean dissolved oxygen (DO₂) near the seafloor were not strongly correlated among themselves, or with other environmental covariates, whereas the remaining covariates displayed multicollinearity, resulting in the following covariate sets: (i) mean surface current velocity and mean EKE, (ii) mean surface salinity, mean chl-a, mean MLT, and variation in surface salinity, (iii) mean SST, mean bottom temperature, and SST variability. All smooth terms for habitat and temporal (date, sun angle) covariates were specified as thin-plate regression splines with an added shrinkage penalty (smooth type = 'ts'), such that non-informative terms shrink to 0 (i.e., no effect), performing automated model simplification (see Marra and Wood 2011).

Models were constructed by including a smooth term for one habitat covariate from each set, and a smooth term for each of the remaining habitat covariates (depth, slope, and mean seafloor DO₂; **Table 2**). Selection among alternate models was achieved by fitting all possible model combinations (i.e., alternate habitat covariates within a set) and selecting among them based on AIC and predictive capacity. Predictive accuracy was calculated as the root-mean-squared error (RMSE) between the observed and predicted CPUE values via cross-validation. As these analyses are preliminary, we focus our discussion of model results on the best-fitting model based on lowest AIC as they typically achieved lowest RMSE also.

Density maps

Maps of Patagonian toothfish density (kg km^{-2}) were created by using the best-fitting model to predict expected catch weight on a 2×2 km resolution grid populated with habitat covariates projected from their native grid using a nearest neighbour protocol. This approach was chosen as it uses the finest scale information available for bathymetry (grid resolution ~ 1.5 km) but maintains the original values and effective resolution of environmental datasets (**Table 2**). When making these predictions, date was set to January-2023 so that predictions represent present day values, sun angle was set at the median value observed throughout the dataset (sun = 0.5), and area-swept was set to 1 km^2 such that predicted catch weights were per km^2 .

Distribution relative to depth and sea surface temperature

Given the expectation of ontogenetic shifts in depth range (Collins et al. 2010) and our focus on the effects of temperature and how it may influence horizontal distribution, we used models to estimate the range of depths, and temperature values, occupied by each size-class of Patagonian toothfish considered. We achieved this by extracting the fitted relationship for depth, holding all other covariates constant, and identified the range of depths that corresponded to the narrowest contiguous interval where the area under the fitted depth function accounted for 90% of the total area. Uncertainty in the resultant depth limits was quantified via posterior simulation using the gam.mh function in mgcv (Wood 2015). The same procedure was applied to smooths for temperature.

Results

Cohorts and size distributions

Size distributions of Patagonian toothfish captured in groundfish surveys were indicative of sporadic recruitment of juvenile fish at Shag Rocks, with 1+ age (≤ 25 cm) cohorts present in seven of the ten surveys from 1987 to 2003, followed by a seeming absence of 1+ cohorts captured in surveys over the following years until 2019 (**Figure 2**). However, 2+ age (26-37 cm) cohorts were often present in years in which there were no notable 1+ cohorts in the previous year (i.e., 2006, 2010, 2012; **Figure 2**), suggesting that sampling may not adequately capture 1+ size fish in all years, possibly due to gear selectivity or the spatio-temporal patchiness of aggregations of 1+ fish. Year-class cohorts were frequently present in sequential survey years, with particularly dominant cohorts first detected in 1990, 2003, 2010, and 2019 forming the majority of fish captured at Shag Rocks over the subsequent 2-5 years (**Figure 2**). Year-classes were often distinct for ages 1+ to 5+ but became hard to distinguish for fish larger than ~ 60 cm (**Figure 2**), most likely due to widening size distributions as fish age, making individual cohorts less distinct, and ontogenetic movement of fish into water deeper than is typically sampled during groundfish surveys (500m depth). In comparison to Shag Rocks, cohorts were rarely distinct at South Georgia, most likely due to overall lower abundance of juveniles, and the predominance of larger fish, typically captured in deeper water around the South Georgia shelf edge (**Figure 2**). Despite that, the strong 1990 year-class recorded at Shag Rocks was also found during South Georgia surveys and was present there as the numerically dominant size-class from 1990 to 1994 (**Figure 2**), indicating that while recruitment at South Georgia is less than that at Shag Rocks, it could be an important avenue of overall recruitment in particular years.

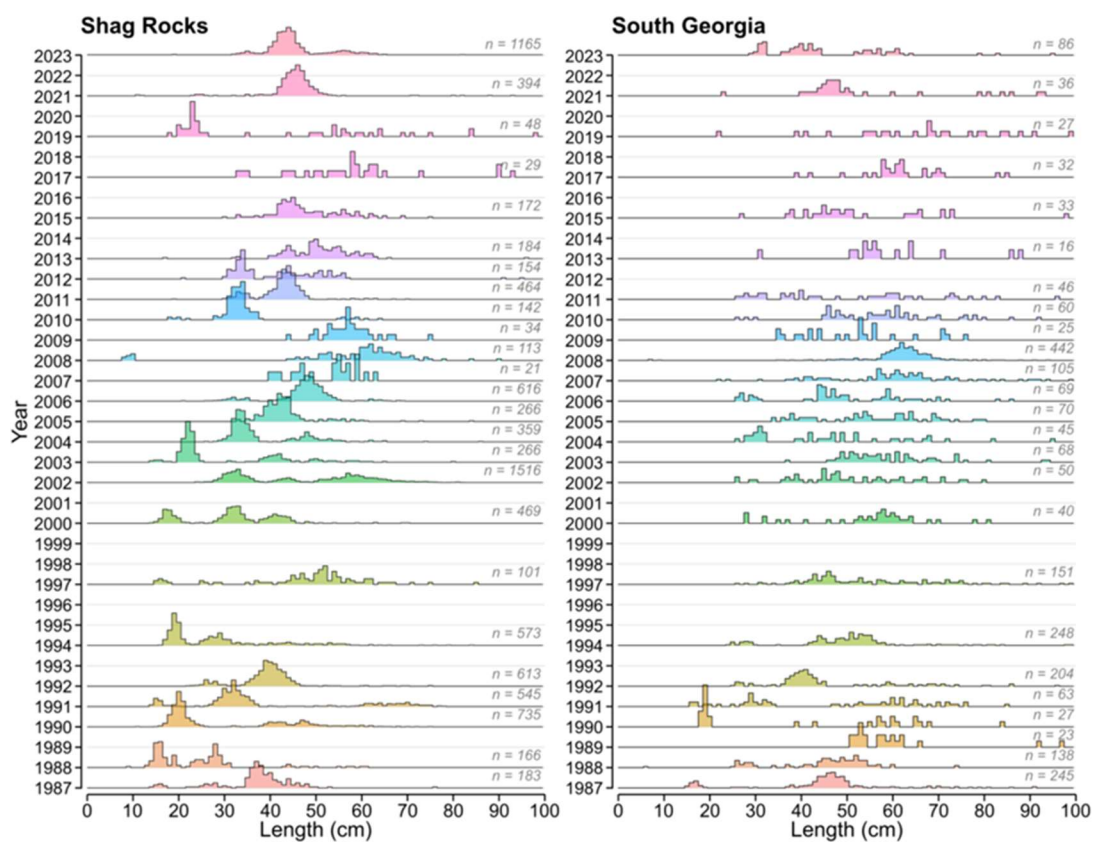


Figure 2. Ridgeline plot showing the size distributions of Patagonian toothfish (*Dissostichus eleginoides*) caught on the Shag Rocks and South Georgia shelves during groundfish surveys from 1987 to 2023. Note that histogram heights are scaled according to the total number of fish caught within each survey, provided in grey text to the right of each panel, and therefore do not necessarily reflect cohort strength/abundance, but rather the contribution of those size classes relative to all other fish captured in a particular year.

Survey-averaged CPUE of the smallest size-classes varied by more than three orders of magnitude at Shag Rocks, varying from an anomalously high value of 1000 kg km⁻² in 1990 to zero in multiple years between 2004 and 2017 (**Figure 3**). Between 1987 and 2003 CPUE of 1+ fish typically measured 1-20 kg km⁻², whereas mean CPUE values greater than 1 kg km⁻² were not encountered again until 2019 (**Figure 3**), suggestive of a long-term, or periodic, decline in CPUE of this age class at Shag Rocks, with broadly similar patterns observed on the South Georgia shelf (**Figure 4**). Survey-average CPUE of 2+ fish (26-37 cm) was less variable measuring ~ 50-200 kg km⁻² across most years between 1987 and 2006, albeit with much lower values in 1997 and 2003, along with an apparent declining trend overall (**Figure 3**). From 2006 onwards CPUE became less predictable, with alternating periods of absent or low CPUE (2007-2009, 2013-2021) followed by periods characterised by CPUE typical of those recorded prior to 2006 (2010-2012, 2023; **Figure 3**). This pattern was also evident at Shag Rocks to some extent in 3+ fish, delayed by 1 year relative to the 2+ size class, although individual years (i.e., high CPUE of 3+ fish resumed in 2021, whereas the 2019 2+ CPUE remained low) were suggestive of alternate periods of low (3+: 2007-2010, 2017-2019) and high (2011-2015, 2021-2023) CPUE. At South Georgia, CPUE of the 2+ size-class was also relatively high until 2006, albeit lower in absolute value than at Shag Rocks, but declined following 2006 with lower CPUE prevailing until 2021 (**Figure 4**). At both Shag Rocks and South Georgia, the most recent survey in 2023 recorded the highest CPUE of 2+ and 3+ size-class fish in more than a decade (**Figure 4**).

For larger size classes (4+: 48-57 cm, 5+: 58-66 cm and 6+/adults: > 66 cm) CPUE has been broadly consistent through time at Shag Rocks (**Figure 3**), suggesting that variability exhibited in younger age-groups is less apparent in later age-groups/size-classes which may be indicative of dispersal from Shag Rocks. However, CPUE of 4+ and 5+ size-classes at South Georgia decreased in 2009/2010 compared to the previous 10-years of surveys, which corresponds to the 2007 transition observed in 2+ and 3+ fish observed at Shag Rocks and South Georgia, indicative of potentially stronger carry-over effects among years at South Georgia than Shag Rocks (**Figure 4**).

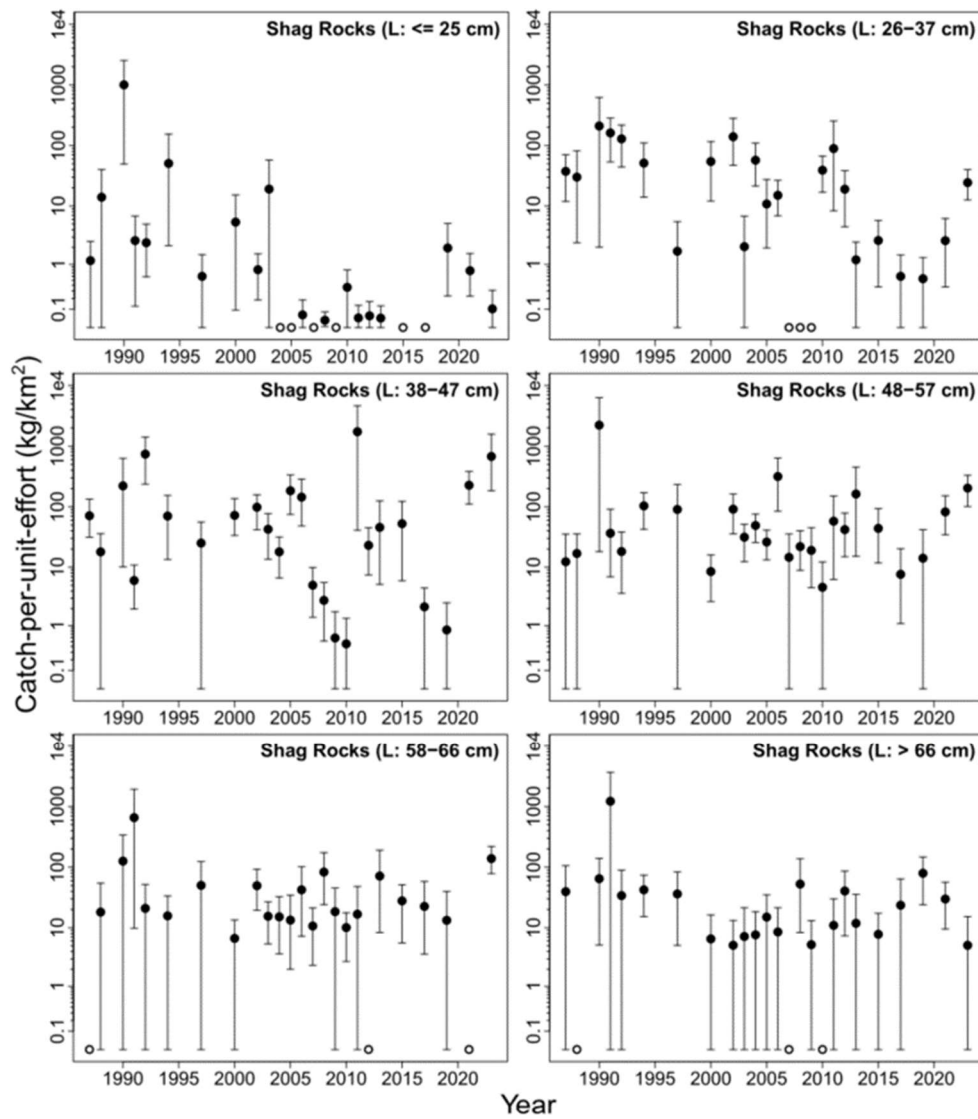


Figure 3. Catch-per-unit-effort (CPUE) of different size-classes of Patagonian toothfish (*Dissostichus eleginoides*) captured during groundfish trawls performed at Shag Rocks between 1987 and 2023. Each size-class roughly corresponds to putative age groups, ranging from 1+ (≤ 25 cm) to 5+ (58–66 cm) age groups, as well as larger juveniles and adult fish (> 66 cm). Values correspond to the survey-mean CPUE based on trawl-specific CPUE, calculated as catch biomass divided by the area swept by trawl gear, with error bars showing the bootstrapped 95% confidence interval of the mean. Years in which no fish were captured in a particular size group are indicated by hollow points, and lower confidence interval limits that equalled zero are clipped at 0.05 to enable plotting on a log-scale.

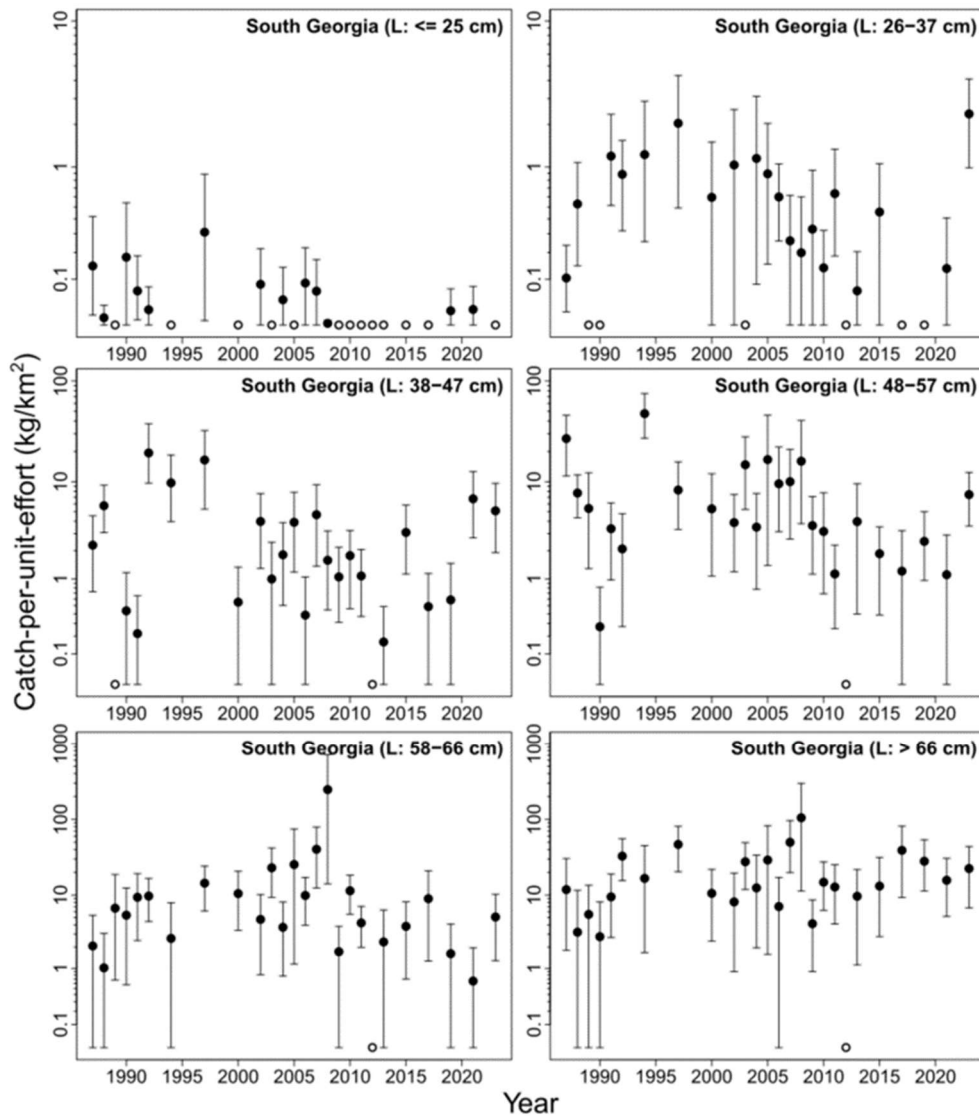


Figure 4. Catch-per-unit-effort (CPUE) of different size-classes of Patagonian toothfish (*Dissostichus eleginoides*) captured during groundfish trawls performed on the South Georgia shelf between 1987 and 2023. Each size-class roughly corresponds to putative age groups, ranging from 1+ (≤ 25 cm) to 5+ (58–66 cm) age groups, as well as larger juveniles and adult fish (> 66 cm). Values correspond to the survey-mean CPUE based on trawl-specific CPUE, calculated as catch biomass divided by the area swept by trawl gear, with error bars showing the bootstrapped 95% confidence interval of the mean. Years in which no fish were captured in a particular size group are indicated by hollow points, and lower confidence interval limits that equalled zero are clipped at 0.05 to enable plotting on a log-scale.

Climate variability

Over the groundfish survey time-period (1986-2023) sea surface temperatures at Shag Rocks and South Georgia have warmed in all seasons, with a higher pace of warming on the South Georgia shelf than at Shag Rocks. In both locations, warming is greatest during the spring (Sep-Nov) and summer (Dec-Feb) seasons (**Figure 5**). Patterns of SST are broadly similar between Shag Rocks and South Georgia, and despite a long-term increasing trend in average SST, periods of cooler summers/autumns (Dec-Feb & Mar-May; 2013-2017) are evident, along with cooler winters (Jun-Aug; 2001-2005, 2016-2020) relative to the long-term trend (**Figure 5**).

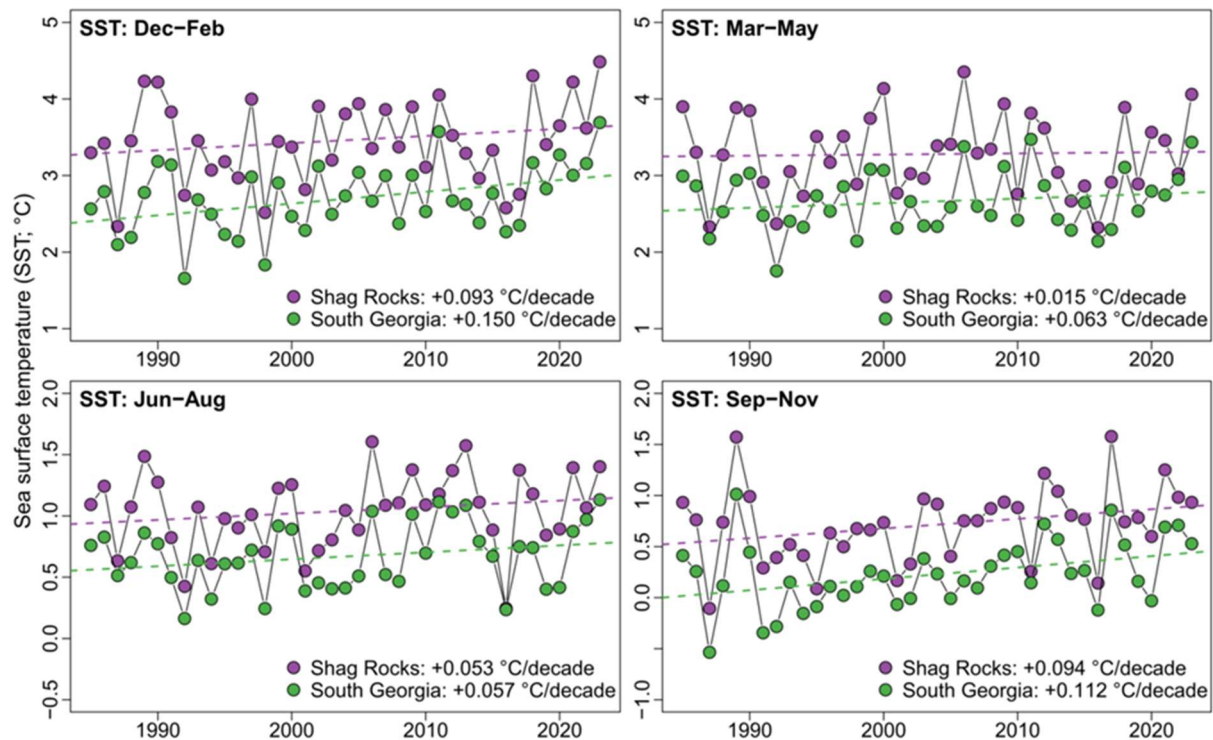


Figure 5. Seasonally averaged sea surface temperature (SST) plotted through time for SST on the South Georgia and Shag Rocks shelves. Dashed lines show a simple linear relationship fitted to the mean values (points), with the corresponding rate of change provided in the figure legend.

Distribution models

Spatial patterns of Patagonian toothfish biomass consistently showed relationships with depth and mean SST across all size-classes (**Table 3**). A positive monotonic relationship with seabed slope was included in most models across size classes but was weaker for smaller size classes (≤ 25 and 26-37 cm), and stronger for two of the larger size-classes (48-57 cm and 58-66 cm; **Table 3**). A generally negative relationship with mean eddy kinetic energy was also retained in models for some size classes, indicative of higher densities in less dynamic locations, and a modal relationship was included with respect to mean mixed layer thickness (MLT) for the smaller size classes, indicating higher densities in locations characterized by moderate surface stratification (**Table 3**). However, estimated effects for EKE and MLT on toothfish density were minor in comparison to depth, slope and SST.

Table 3. Summary of best-fitting distribution models for each size class of Patagonian toothfish (*Dissostichus eleginoides*). Covariate relationships are summarised via symbols to indicate monotonically positive (↗), or negative relationships (↘), or non-linear modal relationships (∩). Blank entries indicate the covariate smooth was not included and/or its effects were shrunk to zero based on smoother regularization penalty. The effective degrees of freedom of the fitted covariate smooth for each term is provided in []. Summary statistics include deviance explained (D²) and normalized root-mean-squared error (nRMSE) of cross-validated model predictions, which varies from 0 (perfect prediction) to 1 (no better than a null model). Covariates given via initialisms are mean sea surface temperature (SST), mean eddy kinetic energy (EKE), mean mixed layer thickness (MLT) and mean seafloor dissolved oxygen concentration (DO₂).

Size-class	Covariate								D ²	nRMSE
	Time	Sun	Depth	Slope	SST	EKE	MLT	DO ₂		
≤ 25	↘ [0.9]	-	∩ [4.6]	↘ [0.6]	∩ [3.4]	-	∩ [2.9]	↘ [0.7]	0.90	0.75
26 – 37	↘ [0.9]	↗ [0.7]	∩ [5.5]	↘ [0.3]	∩ [6.7]	↘ [0.6]	∩ [2.6]	-	0.68	0.89
38 – 47	↘ [0.5]	↗ [0.7]	∩ [5.6]	-	∩ [6.0]	∩ [3.6]	∩ [3.9]	∩ [4.5]	0.73	0.70
48 – 57	↘ [0.9]	-	∩ [6.3]	↘ [1.1]	∩ [5.8]	-	-	↘ [2.3]	0.57	0.74
58 – 66	-	-	↗ [5.8]	↘ [2.0]	∩ [4.4]	↘ [0.9]	-	-	0.53	0.76
> 66	-	-	↗ [5.7]	-	↗ [1.0]	↘ [0.8]	-	↘ [0.7]	0.43	0.77
All	↘ [0.4]	-	∩ [7.2]	↘ [2.0]	∩ [7.6]	↘ [0.9]	∩ [2.5]	↘ [0.6]	0.46	0.95

Depth and mean SST relationships were typically non-linear, modal relationships, indicating a preference for particular depth and temperature regimes, which changed across the size-classes considered (**Figure 6**). Regarding depth, model results were indicative of a shift towards deeper water with age/size, shifting from depths of less than 200 m (peak density at 110 m) for 1+ fish and 2+ fish, to depths of 200-400 m (peak density at 300 m) in 2+, 3+ and 4+ fish, followed by a transition to waters deeper than 400 m in 5+ and 6+/adult fish (**Figure 6**). Although densities were highest in 200-400 m water for 2+ to 4+ fish, depth relationships estimated for each of these size-classes were also suggestive of non-negligible densities at greater depths (**Figure 6**).

Modal relationships with respect to mean SST also prevailed across size-classes, with 1+ to 3+ fish estimated to only occur in locations with annual mean SST > 1.8°C, an effect which remained for all but the largest size class but modified such that increasingly higher relative densities were predicted to occur at cooler locations (**Figure 6**). For the largest size-class, a monotonic relationship was fitted, suggesting both a general increase in density with mean SST, and that fish of this size occur across the temperature range exhibited at South Georgia and Shag Rocks (**Figure 6**). It is worth noting that an annual mean SST of 1.8°C divides the Shag Rocks and South Georgia shelf areas, and so this relationship may also be a proxy for biogeographic (i.e., alternate prey) and/or other oceanographic (salinity, productivity) factors that characterize these areas.

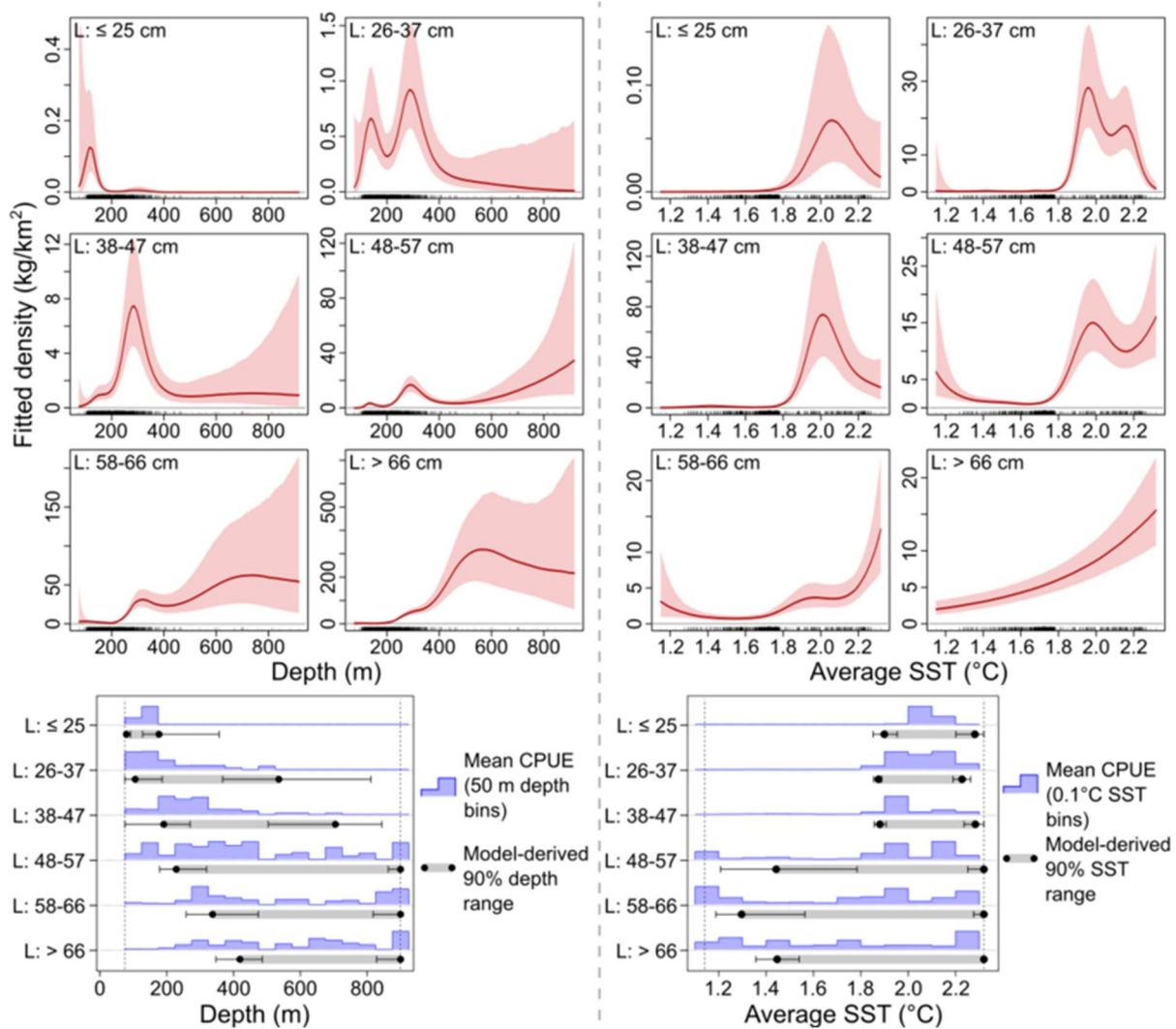


Figure 6. Model-estimated relationships for depth and mean sea surface temperature (SST) derived from models fitted to catches of Patagonian toothfish (*Dissostichus eleginoides*) size-classes at South Georgia and Shag Rocks. Relationships shown are the mean and 95% confidence interval (shading) of the fitted smooth for depth (left column) and mean SST (right) holding all other terms constant. Lower panels show the model-derived interval of depths and SST whereby the area under the fitted relationship equals 90% of the total as a proxy for the most prominent depths and temperatures occupied by each size class. Lower panels also show a visual representation of the raw data in the form of average CPUE binned by depth (50 m depth bins) and SST (0.1°C bins) as a visual comparison to the model-derived depth and SST intervals.

Discussion

This preliminary study, which utilises 28 surveys over 27 years, provides new insights into the distribution of juvenile (pre-recruit) Patagonian toothfish, reinforcing the importance of the Shag Rocks shelf for cohorts 1+ to 3+ identified in previous studies (Collins et al. 2007; Belchier & Collins, 2008). Spatial patterns of Patagonian toothfish biomass consistently showed relationships with depth and annual mean SST across all size-classes. Depth is an important factor, with Patagonian toothfish showing a distinct ontogenetic bathymetric migration even within the first two to three years. A bigger-deeper trend is common amongst scavenging fish (Collins et al. 2005), but juvenile toothfish are predators rather than scavengers (Collins et al. 2007).

The strong inter-annual variability seen in 1+ and 2+ fish on the Shag Rocks shelf was not apparent in the older age-classes, which may be due to dispersal of fish as they grow and move downslope. 1+ fish were particularly associated with the shallow, central part of the Shag Rocks shelf and with mean annual SST of around 2.1°C. Over the groundfish survey time-period SST has increased at both South Georgia and Shag Rocks, most rapidly at the former. For both locations, the rate of warming is greatest during austral spring and summer. Despite a long-term increasing trend in average SST, periods of cooler summers/autumns occurred in some years and cooler winters in others. However, it is not clear if there is a functional relationship between the distribution of Patagonian toothfish and SST, or if SST is a proxy for other factors. We note that the long-term annual mean SST threshold of 1.8°C, which divides areas of high and low toothfish abundance, aligns with the geographic division between Shag Rocks and South Georgia shelves. This suggests SST relationships may also serve as a proxy for biogeographic (i.e., alternate prey) and/or other oceanographic (salinity, productivity) factors that characterize these areas and warrant further consideration.

We reiterate that these are preliminary analyses, and we acknowledge caveats and uncertainties such as spatially/seasonally constrained sampling, and variability of data across the life stages with little being available for the egg/larval stages. However, this initial work provides a useful foundation from which we will determine species-environment relationships for toothfish in subareas 48.3 and 48.4, including different life history stages. This will offer insights into important determinants of distribution, with our overall aim to inform the development of climate response options for the management of toothfish fisheries. Below we outline next steps for the project, and we welcome input and engagement from WG-FSA:

- Species-environment relationships – extend the analysis to include:
 - Subarea 48.4
 - Environmental relationships and fisheries CPUE
 - Antarctic toothfish (*D. mawsoni*)
 - Potential larval retention modelling (e.g. Brigden, 2019);
- Use the species-environment relationships together with projections of future climate conditions to assess potential changes to suitable habitat;
- Undertake a risk assessment of climate-driven change to toothfish populations in subareas 48.3 and 48.4.

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Annex

Table A1. Summary of bottom-trawl surveys used in analyses of Patagonian toothfish (*Dissostichus eleginoides*) distribution. All values presented are after data-cleaning and represent sample sizes entering analyses. Design abbreviations: SRS = stratified random sample, RAD = radial, DW = deepwater trawl surveys.

Survey	Date start	Date end	Gear	Design	Trawls
SG87	29-Nov-86	17-Dec-86	B-454 OT	SRS	104
SG88	19-Dec-87	12-Jan-88	P32/36 OT	SRS	112
SG89	1-Feb-89	14-Feb-89	P32/36 OT	SRS	55
SG90	6-Jan-90	26-Jan-90	HC120 OT	SRS	68
SG91	22-Jan-91	11-Feb-91	FP120	SRS	77
SG92	3-Jan-92	26-Jan-92	FP120	SRS	81
SG94	4-Jan-94	8-Feb-94	FP120	SRS	81
SG97	2-Sep-97	29-Sep-97	FP120	SRS	55
SG00	16-Jan-00	30-Jan-00	FP120	SRS	41
SG02	12-Jan-02	1-Feb-02	FP120	SRS	63
SG03	7-Jan-03	31-Jan-03	FP120	RAD	38
SG04	7-Jan-04	5-Feb-04	FP120	SRS	64
SG05	7-Jan-05	25-Jan-05	FP120	SRS	42
SG06	3-Jan-06	1-Feb-06	FP120	SRS	66
SG07	27-Aug-07	21-Sep-07	FP120	SRS	49
SG08	16-Apr-08	30-Apr-08	FP120	SRS	70
SG09	15-Jan-09	23-Jan-09	FP120	SRS	73
SG10	15-Jan-10	24-Jan-10	FP120	SRS	75
DW10	29-Jan-10	31-Jan-10	FP120	DW	6
SG11	26-Jan-11	6-Feb-11	FP120	SRS	87
SG12	26-Jan-12	29-Jan-12	FP120	SRS ^a	22
SG13	22-Jan-13	29-Jan-13	FP120	SRS	68
SG15	13-Jan-15	23-Jan-15	FP120	SRS	77
SG17	30-Jan-17	7-Feb-17	FP120	SRS	72
DW19	5-Feb-19	5-Feb-19	FP120	DW	3
SG19	27-Jan-19	5-Feb-19	FP120	SRS	73
SG21	8-May-21	28-May-21	FP120	SRS	76
SG23	1-Feb-23	10-Feb-23	FP120	SRS	75

a: 2012 survey was incomplete, with sampling only on Shag Rocks and the NW South Georgia shelf